Regeneration in tropical eucalypt forest on Melville Island

by

Roderick John

R. J. Fensham B. Sc. (Hons.)

submitted in fulfillment of the
requirements for the degree of

Doctor of Philosophy

UNIVERSITY OF TASMANIA

HOBART

SEPTEMBER 1990

Dept of Geog & Env Stud

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except when due reference is made in this thesis.

Roderick Fensham

TABLE OF CONTENTS

ACKNOWLEDGEMENTS i

ABSTRACT iii

LIST OF FIGURES vi

LIST OF TABLES viii

LIST OF PLATES x

CHAPTER 1 INTRODUCTION 1

1.1 Forest regeneration 1
1.2 Regeneration in tropical savanna 3
1.3 Thesis aims and structure 5
1.4 Geographical background 9
1.4.1 Study locality 9
1.4.2 Climate 9
1.4.3 Geology, geomorphology and soils 11
1.4.4 Vegetation 13
1.4.5 Fire 14

CHAPTER 2 ENVIRONMENTAL CONTROL OF OPEN VEGETATION GRADIENT ON WESTERN MELVILLE ISLAND 17

2.1 Introduction 17
2.2 Methods 19
2.2.1 Melville Island survey 19
2.2.2 Root excavation 23
2.3 Results 24
2.3.1 Indirect gradient analysis of Melville Island vegetation patterns 24
2.3.2 Direct gradient analysis of Melville Island vegetation patterns 30
2.3.3 Root excavation 43
2.4 Discussion 44

CHAPTER 3 PATTERNS AND DETERMINANTS OF WOODY GROWTH IN THE TROPICAL EUCALYPT FOREST 55

3.1 Introduction 55
3.2 Methods 56
3.2.1 Woody sprout growth 56
3.2.2 Xylem pressure potential 58
3.2.3 Response to fertilizer 58
3.2.4 Clipping versus burning 58
3.2.5 Mature tree growth 59
3.2.6 Analytical methods 59
3.3 Results 61
3.3.1 Generalized patterns of woody sprout growth 61
3.3.2 Species growth patterns 66
3.3.3 Comparisons between sites 67
3.3.4 Xylem pressure potential 68
3.3.5 Response to fertilizer 70
3.3.6 Clipping versus burning 70
3.3.7 Mature tree growth 70
4.3 Discussion 74

CHAPTER 4 INTERACTIVE EFFECTS OF FIRE AND SITE FACTORS IN TROPICAL EUCALYPT FOREST 82

4.1 Introduction 82
4.1.1 Background 82
4.1.2 Site history 84
4.1.3 Physical environment 86
4.2 Methods 86
4.2.1 Sampling procedure 86
4.2.2 Analytical methods 87
4.3 Results 88
4.3.1 Environmental determinants of vegetation gradients 88
4.3.2 Fire and aspect effects on species composition 91
4.3.3 Fire and aspect effects on vegetation structure 95
4.3.4 Fire effects on woody sprout density 97
4.4 Discussion 97

CHAPTER 5 STAND STRUCTURE AND COMPETITION INFLUENCES ON REGENERATION IN THE TROPICAL EUCALYPT FOREST 101

5.1 Introduction 101

5.2 Methods 103
5.2.1 Stand structure 103
5.2.2 Association of saplings in natural canopy gaps 104
5.2.3 Competition experiment 105
5.2.4 Old experimental sites without overstorey 106
5.2.5 Investigations of the lignotuber 107

5.3 Results 108
5.3.1 Stand structure 108
5.3.2 Association of saplings in natural canopy gaps 111
5.3.3 Competition experiment 111
5.3.4 Old experimental sites without overstorey 115
5.3.5 Investigations of the lignotuber 118

5.4 Discussion 123
5.4.1 Competitive influences 123
5.4.2 Can forest structure be maintained under present conditions? 131

CHAPTER 6 PHYTOPHAGOUS INSECT/VEGETATION INTERACTIONS IN THE TROPICAL EUCALYPT FOREST 134

6.1 Introduction 134

6.2 Methods 137
6.2.1 Insect damage 137
6.2.2 Insecticide experiment 141
6.2.3 Phytophagous insect community 142

6.3 Results 145
6.3.1 Insect damage 145
6.3.2 Insecticide experiment 158
6.3.3 Phytophagous insect community 160

6.4 Discussion 176
6.4.1 Comparison with other studies 176
6.4.2 Insect effects on vegetation 180

CHAPTER 7 ECOLOGICAL DETERMINANTS OF SEEDLING SUCCESS IN TROPICAL EUCALYPT FOREST 186

7.1 Introduction 186

7.2 Methods 187
7.2.1 Progress of young seedlings 187
7.2.2 Seedling garden experiment 187
7.2.3 Association of woody species with vegetation pattern 189
7.2.4 Effects of leaf litter on seedlings 189
7.2.5 Allelopathic effects of *Eucalyptus tetrodonta* leaves on tree seedlings 190

7.3 Results 191
7.3.1 Progress of young seedlings 191
7.3.2 Seedling garden experiment 195
7.3.3 Association of woody species with vegetation pattern 197
7.3.4 Effects of leaf litter on seedlings 201
7.3.5 Allelopathic effects of *Eucalyptus tetrodonta* leaves on tree seedlings 201

7.4 Discussion 203

CHAPTER 8 GENERAL DISCUSSION 206

8.1 Summary of findings and conclusion 206

8.2 The regeneration process 213

REFERENCES 218

APPENDICES 248

Appendix 1 Correlation of vegetation features and environmental variables for the entire Melville Island data set 248

Appendix 2 Correlation of vegetation features and environmental variables for forest plots only 250

Appendix 3 Soil chemical attributes 252

Appendix 4 Insect damage according to damage type 253

Appendix 5 Insect taxa in samples 259

ACKNOWLEDGEMENTS

During the field work phase of my project, Dave Bowman, Bruce Wilson, Jeremy Russell-Smith and Clyde Dunlop provided much stimulus and encouragement. Clyde and his Herbarium staff made it possible to learn the unpublished flora of Melville Island.

The implementation and perpetuation of this project was a hair-raising bureaucratic balancing act that was only possible through the support and enthusiasm of several people. Without Dave Bowman's deft administration and financial support, the project could never have got off the ground. Dave's enthusiasm for ecology and learning in general was an important inspiration. The Conservation Commission of the Northern Territory provided the infrastructure during the first year, through their forestry operation on Melville Island. For this period, Bill Freeland, Merv Haines, Ron Hooper and Tim McGuffog were instrumental. The Tiwi Land Council took over the forestry operation during the second year and John Hicks, Greg Sutton and the members of the Council allowed the project to continue, despite the withdrawal of the Conservation Commission from the island.

Many visiting friends helped with field work. Dave Bowman, Judith Gallen, Leonie McDough and Bruce Wilson kindly organised the ferrying of gear between Melville and the mainland.

Melville Island is home for the Tiwi and they allowed me to live and work on their island for two years. Sharing life with these people had a profound influence on my life and gave me a fresh perception of the bush.

The Land Conservation Unit of the Conservation Commission conducted some of the soil analyses. Alan Andersen from CSIRO, Darwin, Gordon Gross, from the S. A. Museum, and Catriona McPhee, from the Museum of Victoria examined insects. Neil Gibson and Bruce Wilson got me started with computing. Zhenjie Lin wrote the computer programs for part of the analysis in Chapter 6.

Jamie Kirkpatrick has been a great inspiration and friend since I first started studying the bush in 1983. He gave encouragement and feedback throughout the project and particularly during the 'writing up' phase in Hobart. Jamie and Dave Bowman were my excellent formal supervisors for the project.

Many colleagues and friends participated in proof reading and the examiners of this thesis made many useful crticisms.

Lisa put in the late nights that always seem necessary during the dying stages of episodes such as this one.

I thank all of these people immensely.

ABSTRACT

The eucalypt species of the evergreen savanna forest in monsoonal Australia have a population structure characterized by mature trees, an abundance of short stems in the ground layer and low densities of saplings. Other common trees of these forests, such as the broadleaved species, are almost exclusively represented by these short woody sprouts. The distinctive structure of the eucalypt forests begs the question as to how these forests are perpetuated. This study seeks to examine tree regeneration in the eucalypt forests of Melville Island in the wet-dry tropics of Australia. The first part of the thesis adresses the influence of the physical environment on regeneration by examining edpahic influences on vegetation structure, growth rates and fire response. The second part of the thesis concentrates on the evergreen eucalypts forests and examines possible causes for the supression of woody sprouts.

An attempt was made to define the soil moisture conditions across the range of savanna types. However, elucidating the relationship between edaphic conditions and vegetation patterns is difficult because of the effect of rockiness and soil texture on root penetration. It is reasonably certain that evergreen eucalypts are excluded from one intensively studied site because a clay layer impedes root growth. This low forest is dominated by semi-deciduous eucalypts and the growth of all woody sprouts is slower than in the tall forest. Despite less vigorous growth, broadleaved tree species, such as *Terminalia ferdinandiana* and *Planchonia careya,* occupy the mid-canopy at this site. It is suggested that the tall evergreen eucalypts, *Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta,* suppress the growth of other tree species.

Overwood suppression is evident within the tall forest. Tree seedlings grew more rapidly under killed trees than live overwood. Furthermore, clearfelled sites develop saplings although the replacement of the tree canopy occurs sporadically. Few eucalypt saplings developed in an extensive experiment designed to examine the influence of eucalypt and wattle trees and herbage on tree

regeneration. The saplings of two tree species were weakly associated with natural canopy gaps. The saplings of three other species had no such association. It is suggested that underground organs of middle-age and with well developed root systems are the most likely to become trees. Underground organs are extensively damaged by termites, and relief from this form of herbivory may contribute to the accession of saplings.

It is demonstrated that moisture conditions, below 50 cm, are generally adequate for tree growth throughout the year. This helps to explain why the new growth of woody sprouts after fire, occurs during the driest months. These ground layer stems stop growing when water is abundant during the wet season. The hypothesis that competition for moisture provides the mechanism of overwood suppression is difficult to equate with these facts.

The hypothesis that competition for nutrients controls the suppression of young trees is not supported by an experiment where woody sprouts showed no response to fertilizing.

Patterns of insect abundance and damage levels indicate that the growth of woody sprouts is not tuned to the activities of phytophagous insects. There was no relationship between stem height and levels of insect damage. Furthermore, experimental protection of plants using pesticide did not increase growth. Thus, it seems that suppression of tree stems cannot be attributed to insects.

Shredded *Eucalyptus tetrodonta* leaves suppressed seedlings of the same species when applied to pots in a nursery experiment. It is suggested that allelopathic interactions may be important for suppressing regeneration.

Relief from fire is another factor that contributes to tree regeneration. However, the effect of this agent on forest structure seems dependent on certain site conditions. The development of tree saplings in a rocky eucalypt forest after longterm fire protection contrasts with limited sapling development in another fire protected forest on deep soil.

Many features of the regeneration process remain unclear but this thesis provides sufficient evidence to postulate a comprehensive model describing a common regeneration strategy in tropical eucalypt forest.

Figures

Figure 1.1 Melville Island and Bathurst Island locality map 10

Figure 2.1 Environmental and vegetation vectors through ordination space 29
Figure 2.2 Transects on Melville Island survey ordination space 31
Figure 2.3 Moisture characteristic curves 32
Figure 2.4 Predictive accuracy of matric potential values 32
Figure 2.5 Rainfall, Nguiu, Bathurst Island 33
Figure 2.6 Transect 1 34
Figure 2.7 Transect 2 35
Figure 2.8 Transect 3 37
Figure 2.9 Transect 4 38
Figure 2.10 Transect 5 39
Figure 2.11 Transect 6 40
Figure 2.12 Tree species distributions 50

Figure 3.1 Matric potential cycles and woody sprout growth 62
Figure 3.2 Breakaway stem growth 65
Figure 3.3 Matric potential cycles and mature tree growth 71
Figure 3.4 Hythergraph, Pularumpi, Melville Island 77

Figure 4.1 Solar Village locality map 85
Figure 4.2 Solar Village ordination result 88

Figure 5.1 Size class histograms, eucalypt forest 109
Figure 5.2 Competition index histograms 112
Figure 5.3 Growth of *Eucalyptus miniata* sapling 114
Figure 5.4 Size class histograms of sapling regeneration on clearfelled blocks 116
Figure 5.5 Sapling densities vs distance from clearing 118
Figure 5.6 Relationship between lignotuber size and stem height 120

Figure 6.1 Insect damage through post-emergence year 151
Figure 6.2 Other damage through post-emergence year 159
Figure 6.3 Abundance distribution of major insect groups for individual plant species 162
Figure 6.4 Mean abundance distribution of major insect groups 172
Figure 6.5 Proportion of major phytophagous insect groups 180

Figure 7.1 Plan of seedlings and surrounding trees 192
Figure 7.2 Mortality of tree seedlings 193
Figure 7.3 Height of tree seedlings in experimental gardens 196
Figure 7.4 Mortality of tree seedlings in experimental gardens 198
Figure 7.5 Classificatory groups in open forest 199

Figure 8.1 Regeneration cycle of *Eucalyptus miniata* 214

Tables

Table 2.1 Percentage frequency according to TWINSPAN group 25
Table 2.2 Root distribution 44

Table 3.1 Distribution of species x growth strategy 67
Table 3.2 ANOVA of relative growth rate 68
Table 3.3 Xylem pressure potential between sites and lifeforms 69
Table 3.4 Diameter and diameter increment of mature trees 70

Table 4.1 ANOVA of environmental variables 90
Table 4.2 Percentage moisture in soil 91
Table 4.3 ANOVA of species richness 91
Table 4.4 ANOVA of species distribution 92
Table 4.5 Percentage cover of species responding to fire-aspect interactions 94
Table 4.6 ANOVA of saplings 96
Table 4.7 Density of saplings responding to fire-aspect interactions 97
Table 4.8 ANOVA of woody sprouts 98
Table 4.9 Density of woody sprouts responding to fire-aspect interactions 99

Table 5.1 Densities of breakaway saplings according to experimental treatment 113
Table 5.2 Tree densities in tree killed plot at Yapilika 115
Table 5.3 Stem height according to lignotuberous features 121

Table 6.1 Insect damage 146
Table 6.2 ANOVA of proportional damage term 148
Table 6.3 Correlation between growth rate and damage 154
Table 6.4 Comparison of damage between sites 156
Table 6.5 ANOVA of insect groups 170
Table 6.6 Insect species according to host plant 174
Table 6.7 Review of insect herbivory in Australia 178

Table 7.1 Soil moisture in gardens 194
Table 7.2 Percentage frequecy of plant species in classificatory groups 200
Table 7.3 Frequency of lignotuberous trees by classificatory group 201
Table 7.4 Plant performance according to mulching treatment 202

Plates

Plate 2.1 Root system of *Eucalyptus tetrodonta* 47

Plate 3.1 Lignotuberous stem of *Buchanania obovata* with fruit 80

Plate 5.1 Lignotuber of *Planchonia careya* 119
Plate 5.2 Lignotuber of *Eucalyptus nesophila* 119
Plate 5.3 *Eucalyptus nesophila* sapling without taproot 122
Plate 5.4 *Eucalyptus tetrodonta* saplings regenerating from rhizomes 127
Plate 5.5 Dead lignotuber 127
Plate 5.6 Tap root destroyed by termites 129

Plate 6.1 Insect galls on *Buchanania obovata* 157
Plate 6.2 Mining damage on *Acacia aulacocarpa* 157

Plate 7.1 *Eucalyptus miniata* seedlings 194

CHAPTER 1 INTRODUCTION

1.1 Forest regeneration

The decipherment of the regeneration mechanisms of key tree species is critical to understanding the dynamic relations of any forest community (Grubb 1977, Bazzaz 1979). The regeneration process has thus provided a theoretical and practical focus for the study of forest ecosystems throughout the world (eg. coniferous forests, Sprugel 1976, Hett and Loucks 1976; temperate deciduous forests, Lorimer 1983, Runkle 1982, Parker 1986, Nakashizuka 1987; tropical rainforest, Whitmore 1975, Brokaw and Scheiner 1989; temperate rainforest, Veblen 1985). In Australia regeneration has been studied in temperate eucalypt forest (Parsons 1968, Ashton 1981, Abbott and Loneragan 1984, Bowman and Kirkpatrick 1986a, b) temperate rainforest (Cullen 1987, Read and Hill 1988) and tropical rainforest (Webb *et al.* 1972).

Whitmore (1982) argued that the forests of the world, despite their range of floristic and structural complexity, are fundamentally similar because they are sustained by the same regeneration process. This process is characterized by three phases of development: a canopy gap, a building phase that develops in the gap and the mature forest. At a broad level forests may in fact be functionally united. However, this means of generalizing forest dynamics is limited because its acceptance requires extremely broad definitions of the regeneration phases.

Canopy gaps in forests vary from a speck of sunlight penetrating the foliage of a rainforest canopy to the large scale destruction of forest caused by wildfire. The 'Black Friday' fires in southeastern Australia created 'canopy gaps' totalling 1.3 million ha over three days in 1939 (Wetterhall 1975, p 44). Furthermore, the nature of the gap varies according to the agent of disturbance and the type of forest in which it occurs. The overstorey in some forest communities, such as rainforest, are killed by fire and a gap is created. Trees in other forests are well adapted to fire which only results in temporary defoliation. The overstorey in many eucalypt forest types in Australia is not destroyed by fire (Gill 1981, Lacey *et al.* 1982) and unless a tree falls over an effective gap is not created.

The resources that limit regeneration are also important for determining the nature of the building phase. In most rainforest types light is the critically limiting resource with the most important determinant of the composition of the building phase being the size of the canopy gap. Relief from darkness declines as the building phase develops. Some forests are floristically diverse and succession is an important part of the regeneration process. Species of the early building phase create conditions that are suitable for other tree species. In these cases the structure and floristics of the forest are determined by a mosaic of different successional phases (eg. Williamson 1975, Ricklefs 1977, Veblen *et al.* 1979). In forests with one or two dominant tree species, the concept of succession is less relevant although the possibility of cyclic succession cannot be dismissed.

For more open forest types, canopy light is not limiting and the regeneration niche is determined by the availability of other resources. For example, it has been demonstrated that soil moisture limits regeneration in dry subalpine eucalypt forest in Tasmania (Bowman and Kirkpatrick 1986a, b) and the Victorian mallee (Wellington 1984).

During the building phase, the processes occurring are different if regeneration is from seed than if regenerating trees are pre-existing stems. *Eucalyptus regnans* F. Muell. regenerates *en masse* from seed after the creation of a gap by wildfire and the developing forest is single aged (Ashton 1981). Most trees can germinate under the canopy in rainforest but remain as suppressed saplings until a gap is created (Whitmore 1975, Brokaw 1985). Established saplings will take advantage of a newly formed gap more successfully than young seedlings. In fire-prone environments, it is common for plants to develop underground organs that allow the plant to survive the complete removal of above-ground parts and regenerate new stems. The ability to coppice from rhizomes and lignotubers has adaptive significance because the growth rate of stems with established roots exceeds that of developing seedlings. The relative importance of these strategies for any particular forest type is of great functional significance.

1.2 Regeneration in tropical savannas

Tree regeneration in the world's tropical savanna has received scant attention although some authors have addressed isolated features of the process (eg. Hopkins 1963, Lacey 1974, San Jose and Farinas 1983, Bowman 1986, Miyanishi and Kellman 1986). The limited understanding of this process in tropical savannas clearly represents a deficiency in ecological knowledge given the vast area of this biome across the equatorial regions of the globe (Strahler 1975). A considerable portion of the area of these ecosystems have few trees, however, tropical savanna that qualifies as forest in Specht's (1970) structural classification can be identified in the literature and seems to be prominent in Southeast Asia (Ogawa *et al.* 1981, Blasco 1983, Stott 1984) and northern Australia (Story 1976, Gillison 1983).

Vegetative regeneration is prominent in tropical savannas (Sarmiento and Monasterio 1983) but the importance of external influences on the growth and development of tree stems is poorly understood. The importance of edaphic factors as determinants of structural development has been recognised in Australian savanna (Bowman 1988). However, the most complete studies of soil/vegetation interactions in tropical savanna have arisen from South America (synthesized by Sarmiento 1984). In the savanna environment of this continent macro and meso-scale variations can be clearly correlated to edaphic gradients. The implication from this body of research is that intrinsic site conditions are a critical determinant of the differential regeneration potential of various tree species. Most of the South American work implicates soil moisture availability as the major cause of structural pattern. However, studies from Central American tropical savanna suggest that the development of some tree species requires nutrient rich microsites (Kellman 1979, 1985, Kellman and Miyanishi 1982).

Some authors emphasize the importance of fire as an influence on tree growth in tropical savanna. Hopkins (1963) provides evidence that fire promotes lignotuberous regrowth, while Miyanishi and Kellman (1986) indicate that repeated burning can result in the death of lignotuberous shrubs because of the depletion of root starch reserves.

In Africa, fire protection has resulted in the invasion of savanna by closed forest species (Ross-Innes 1972). San Jose and Farinas (1983) demonstrated that fire protection resulted in the accession of tree species as saplings in South American savanna. These studies suggest that fire is a critical factor that inhibits tree regeneration in tropical savannas. Bowman *et al.* (1988a) studied the effects of fire protection in eucalypt savanna vegetation in northern Australia. In this situation there was structural development in both forest and woodland communities, although in the former community most tree development was of short-lived species and there were very few saplings of the overstorey dominants. Thus the available evidence from the eucalypt savanna forest suggests that fire does not critically limit tree regeneration.

Few studies have considered competition as a mechanism for retarding tree regeneration in tropical savanna. The existing work on this subject has considered the dynamics between the grass and tree layers of tropical savanna. There is sparse evidence from quantified studies of competition between these lifeforms (Knoop and Walker 1985) and this conforms to theoretical suggestions of resource partitioning between these fundamental strata of the savanna (eg. Belsky 1990). There is no quantified work on the inhibition of tree regeneration by overstorey, although Bowman (1986) has suggested that the relief of suppressed stems requires relief from overwood competition in tropical Australia.

The process of regeneration is reflected in structural features of the forest. Multi-stemmed woody regrowth arising from underground organs is a prominent feature of the ground layer of the tropical eucalypt forest (Dunlop 1988). Lacey and Johnston (1990) have coined the term woody clumps to refer to multi-stemmed woody plants. This definition includes trees and shrubs. In this thesis the term woody sprouts will refer to the short (less than one metre) multi-stemmed tree regeneration in the ground layer of the tropical eucalypt forest. A characteristic feature of the eucalypt forest is the sporadic and generally infrequent occurrence of saplings (Braithwaite and Estbergs 1985). Occasionally, broadleaved shrubs occupy the midstorey in some forest

types although usually this occurs in forests dominated by semi-deciduous eucalypts (Bowman 1988).

The vegetative regeneration structures of a range of tree species from the tropical open forest of the Top End have been described by Lacey and Whelan (1976). Lignotubers (Carr *et al.* 1984), rhizomes (Lacey 1974) and root suckers (Carr 1972) are common methods of vegetative reproduction in this ecosystem. For a large part of the experimental work reported in this thesis eight common tree species (species nomenclature follows Dunlop (1987) unless otherwise given) were selected for study. These species come from six different plant families and have a range of lifeforms and leaf and phyllode sizes. These species also have a range of regenerative anatomies. *Buchanania obovata, Eucalyptus confertiflora, Planchonia careya, Terminalia ferdinandiana* and *Eucalyptus miniata* all possess lignotubers. All of these species except the latter are deciduous or semideciduous. *Erythrophleum chlorostachys* and *Acacia aulacocarpa* were chosen for study because they are common evergreen species that use root suckers for vegetative regeneration. The former species has large compound leaves and the latter has phyllodes. *Eucalyptus tetrodonta* was also chosen for study and is a widespread dominant evergreen tree that regenerates vegetatively from lignotubers and root suckers.

1.3 Thesis aims and structure

Given that our knowledge of tree regeneration in tropical savanna is fragmented, the present study seeks to examine facets of the tree regeneration process in the eucalypt savanna forests of northern Australia. Chapter 2, 3 and 4 all focus on how edaphic influences interact with other environmental forces to determine structural and regenerative features of the tropical eucalypt forest. Thus these chapters address the following general questions:

1) to what extent can edaphic gradients be correlated with patterns in the structure and composition of the overstorey?
2) can tree growth be related to temporal and spatial patterns in the edaphic environment?
3) do changes in fire frequency have varying effects on structural development in different edaphic environments?

The importance of edaphic controls for determining mesoscale vegetation pattern in the tropical savannas of northern Australia has been documented (eg. Bowman and Minchin 1987, Kirkpatrick *et al.* 1987). Clearly some patterns can be attributed to exogenous control. Relating patterns to the physical environment at a finer scale has proved to be more difficult (eg. Andrew 1986, Bowman *et al.* 1988a). Chapter 2 examines floristic and structural patterns along vegetation gradients within the savanna environment and attempts to determine the extent of edaphic controls on tree regeneration as reflected by the structural features of the forests.

The results of Chapter 2 raise the possibility that much of the pattern within the eucalypt forest results from interactions between endogenous and exogenous factors. Bowman (1988) has previously suggested that some structural variants of the tropical eucalypt forest are a product of interactions between the edaphic environment, plant growth rates and fire. In the light of this probability Chapter 3 examines the nature of the interaction between tree growth rates and edaphic conditions. The first part of this chapter examines woody sprout growth in relation to an edaphic gradient. The second part looks at the influence of soil nutrients on woody sprout growth in an experimental situation.

Fire is almost an annual occurrence in tropical eucalypt forests. Bell (1981) and Braithwaite and Estbergs (1985) have suggested that the absence of saplings in this environment may be a product of the fire regime. Bowman *et al.* (1988a) documented the response of open forest and woodland to fire protection at Munmalary in northern Australia. Sapling development of most species was limited in the fire protected forest at this site. The contrasting response of the forest and woodland to fire protection at Munmalary contributed to Bowman's (1988) suggestion that site/fire interactions need to be invoked to explain structural development. Chapter 4 contributes to our understanding of the influence of fire protection on savanna vegetation and specifically the importance of this relief for sapling development in a geomorphic environment that has not previously been studied.

The second half of the thesis focuses on the regeneration process in savanna forest dominated by evergreen eucalypts on deep red earth soils. This section of the thesis addresses the following general questions:

1) what is the importance of competition as a mechanism for inhibiting the regeneration of woody sprouts?
2) what is the importance of above-ground herbivory as a mechanism for inhibiting the regeneration of woody sprouts?
3) what are the influences on the growth and mortality of tree seedlings?

Studies of seedling establishment in temperate eucalypt forests have determined that overwood suppresses regeneration (eg. Abbott and Loneragan 1984, Bowman and Kirkpatrick 1986a,b, Incoll 1979). Wilson and Bowman (1987) document sapling development in tropical eucalypt forests following the felling of overstorey trees after a cyclone. Other studies suggest that competition is an important functional component of tropical savanna. Clearly the influence of overwood is a likely avenue of exploration for determining the mechanisms of woody sprout suppression.

The partitioning of resource exploitation by the grass and tree components of savanna has been a central axiom for the study of their ecology (Walter 1971, Walker and Noy-Meir 1982, Goldstein and Sarmiento 1987). Knoop and Walker (1985) were able to show that tree growth is inhibited by the grass layer in some African savanna. Chapter 5 presents size class information for forest tree species on Melville Island and continues with an examination of the competitive effects of overstorey, *Acacia* species and herbage on regenerating trees.

Abbott and Loneragan (1984) were able to show that lignotuber size was related to sapling success for jarrah (*Eucalyptus marginata* Donn ex Sm.) in temperate Australian forests. Small lignotubers could not support advanced regrowth. Lignotuber size may reflect root storage reserves. It has been demonstrated that the regenerative ability of aspen (*Populus tremuloides* Michx.) is affected by carbohydrate reserves in the root systems (Tew 1970) and the same relationship has been demonstrated for savanna shrubs in Central America (Miyanishi

and Kellman 1986). It is possible that the sporadic occurrence of saplings in the tropical eucalypt forest is a product of the physiological condition of trees in the ground layer. Chapter 5 includes an examination of the morphological features of lignotubers and root system and attempts to relate these features to sapling success.

Sarmiento *et al.* (1985) suggest that the seasonal growth rhythms of tropical trees may be tuned to avoid periods of intense insect herbivory. During the monitoring of growth (Chapter 3) it was observed that suppressed woody sprouts suffered considerable insect damage. Chapter 6 examines the contribution of insect herbivory to structural pattern. Chapter 3 highlights some unusual features of seasonal growth rhythms in the tropical savanna of Australia. The work reported in Chapter 6 was partly designed in response to the questions raised in Chapter 3 and addresses the hypothesis that the growth rhythms of trees are tuned to the spatial and seasonal activities of phytophagous insects.

The dominance of woody sprouts in the ground layer of the tropical eucalypt forest suggests that trees develop from this lifeform. However, an understanding of the regeneration cycle would be incomplete without knowledge of seedling establishment. Seedlings are rarely observed in the tropical eucalypt forest so opportunities for the study of their natural occurrence are limited. Some eucalypt seedlings were located during the course of this study and Chapter 7 examines the environmental relations of seedling establishment and the factors that influence the success of trees in the early stages of their existence.

Seedlings are more easily manipulated for experimentation than established trees. Chapter 7 includes a field experiment designed to decipher the role of litter leachates as an agent of suppression. The role of live leaf leachates as an allelopathic agent is also examined.

Chapter 8 concludes with a discussion of the factors and processes that contribute to the temporal and spatial pattern of savanna forest trees. The chapter includes a model of the regeneration process and attempts to weigh the importance of the influences affecting this process.

1.4 Geographical background

1.4.1 Study locality

The Tiwi Islands (otherwise known as Melville and Bathurst Island) lie in the Arafura Sea about 40 km from the coast of northern Australia (Fig. 1.1). The larger of these narrowly separated islands is Melville Island, the second biggest offshore island in Australian territory.

The Tiwi Islands are part of that northern portion of the Northern Territory with the popular name 'The Top End'. The Top End is climatically and biogeographically distinct from the deserts that comprise the southern inland portion of the Northern Territory (Bowman *et al.* 1988b) and as such it is a useful colloquialism that will be used throughout this thesis.

1.4.2 Climate

At latitude 11° S, Melville Island is firmly seated in the tropics and is in the hottest region of Australia (Nix 1981). Mean maximum temperature at Milikapiti varies little between 31.1°C in July and 33.8°C in November. Mean minimum temperature variation is somewhat greater with mean values between 18.3°C in July and 24.0°C in November. Hours of daylight vary throughout the year by only 1.5 hours (McAlpine 1976).

Unlike temperature and daylight hours, rainfall is strongly seasonal and is almost totally apportioned to the 5 month wet season. The wet season typically occurs between mid-November and mid-April and receives over 90% of the mean annual rainfall. In terms of total rainfall, the Tiwi Islands are the wettest part of the Top End although mean annual precipitation does vary between rainfall stations, from 1496 mm at Nguiu to 1970 mm at Pularumpi. Wet season rain and dry season drought are annual phenomenon although Taylor and Tulloch (1985) have demonstrated that the timing of the transition between the two dominant seasons, the length of rainless periods during the wet season and the total amount of rain are variable. Generally the

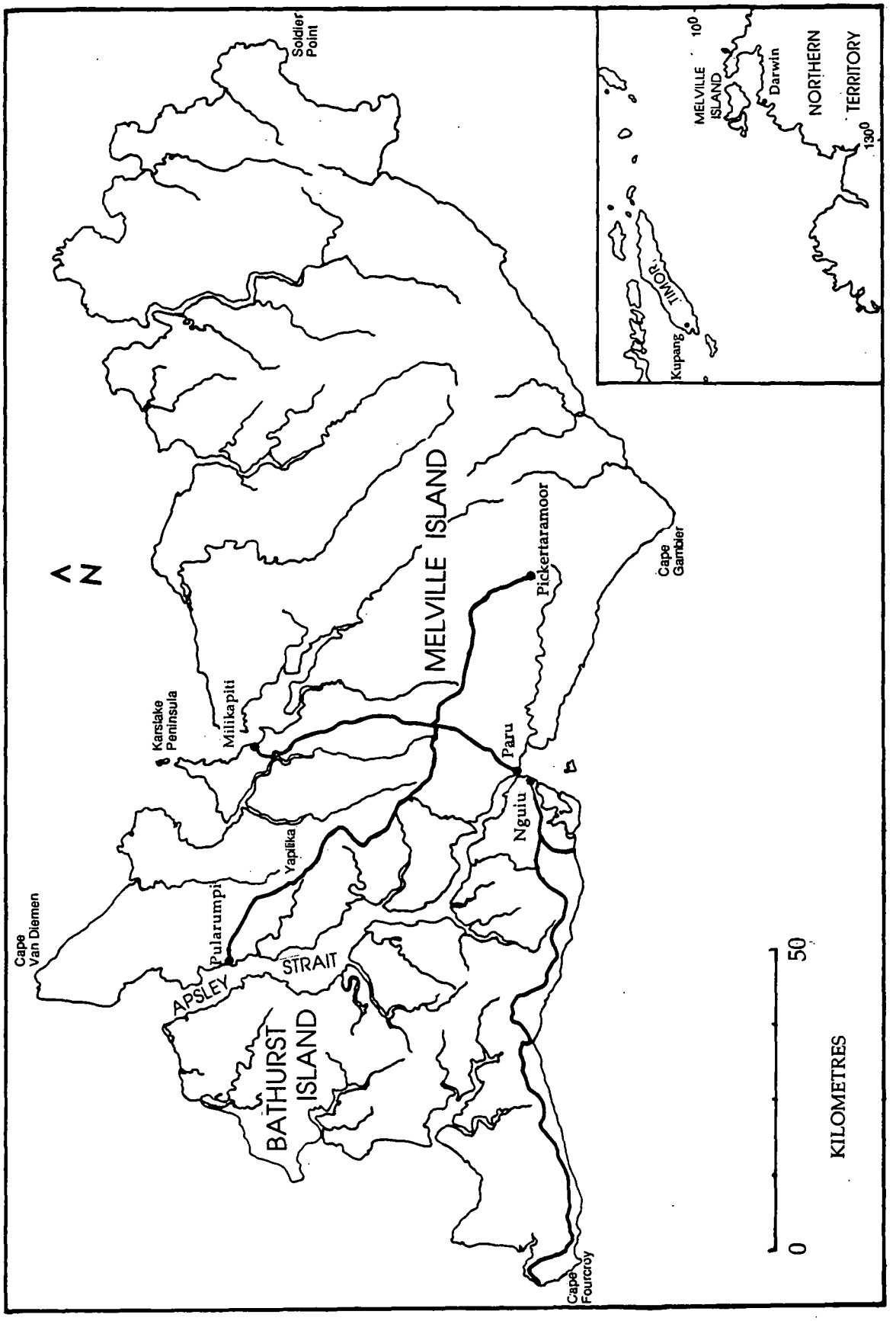


Figure 1.1 Melville and Bathurst Islands showing locations of places mentioned in the text.

seasonal distribution of precipitation on Melville Island is very similar to that of other coastal regions of the Top End. However, catabatic thunderstorm activity is responsible for the highly predictable arrival of wet season rain across the middle of the island about a month earlier than for coastal regions (Keenan *et al.* 1990, Skinner 1990).

Aboriginal people recognise many minor seasons (ANPWS 1980, Haynes 1985, Anonymous 1983, Davis 1989) and Europeans identify the 'buildup' during October and November when temperatures are hottest, humidity high but rain infrequent.

A detailed description of the climate in the coastal region of the Top End is provided by McAlpine (1976).

1.4.3 Geology, geomorphology and soils

Melville Island consists of undulating rises and dissected plateaux and has its highest point a meagre 74 m above sea level. The areas of highest relief are remnants of a Tertiary landform, the Van Diemen Sandstone (Hughes 1976), which is exposed in the sea cliffs near Cape Van Diemen. The major watershed runs east-west near the southern coast (Fig. 1.1). North of the divide there are large areas of sandplain that have been deposited following erosion of the old Tertiary surface. Very recent alluvium has been deposited along creeks, the largest of which flow northward (Fig. 1.1). Regardless of the age of the substratum all soil profiles are strongly weathered and lateritization is a dominant process.

There has been considerable confusion over the concept of laterite and the processes governing its formation (Paton and Williams 1972, Ollier and Galloway 1990) since its inception early last century as a term used to define a material that dried on exposure and was suitable for making bricks (Buchanan 1807). Despite the confusion, the notion of the classic laterite profile has been well accepted. The base of the profile consists of decomposed rock called saprolite that is divided between a pallid zone and an overlying mottled zone. These layers are overlain by a ferruginous zone in which hydroxides of iron and aluminium have been concentrated because of their immobility. In this zone,

ferruginous or bauxitic concretions can be present as a solid mass although they are more usually held in a matrix of soil. A fundamental feature of laterite is the concentration of iron although this phenomenon has never been satisfactorily explained (Selby 1982, p 38-41).

Use of the term laterite is problematic because a precise definition has never been achieved and this is reflected by the range of materials that have been included under this nomenclature. Ollier and Galloway (1990) suggest that a product of this confusion is the overlooked assumption that the lateritic profile formed *in situ*. They argue that there is no genetic connection between saprolite and the ferruginous zone. They provide evidence that the predominant situation involves a detrital origin for the ferruginous zone. There is considerable evidence of sedimentary transport on Melville Island. In fact the described 'classic' laterite profile is rarely evident. It seems that existing substrate profiles are a result of partial denudation of preexisting substrates with or without deposits of clastic material. Continuing and possibly rapid processes of pedogenesis and lateritization further the perplexing farrago of weathering products and stages. Substrate profiles on Melville Island invariably reveal portions of the classic laterite profile. The ferruginous zone can consist of concretionary laterite where nodules are irregular in shape and larger than 2 cm in diameter or pisolithic gravels less than this size. These gravels may represent decomposed fragments of lateritic parent material or may have formed as a result of the lateritic process (Aldrick 1976). A mottled zone is present in some profiles and, as its name suggests, is multi-coloured and textured. The texture of the pallid zone is between soft rock and heavy clay, and is rich in the clay mineral kaolin.

In contrast to many lateritized landscapes duricrusts are not evident on Melville Island and most of the land surface is mantled by red massive earth although yellow and grey earths are also common. Where slopes are greater than 5% soils are shallow and the ground is rocky. Surface soils of the massive earths vary in texture from loamy sand to loam and the structure of the soil profile is highly variable. Deep and undifferentiated sandy loams, duplex soils and all variants in between

are evident. However, soils with weak profile differentiation and an illuvial B horizon of sandy clay loam to light clay texture are common. Gravel and rock layers frequently occur in any part of the soil profile and can be of varying thickness. A range of soil profiles are described by Wells *et al.* (1979), Wells and van Cuylenburg (1978), Wilson (1990) and by Figs. 2.8-2.13 of this thesis.

Wells and van Cuylenburg (1978) report on the nutrient composition of Melville Island soils. They are generally infertile and acid with pH ranging from 4.3 to 5.7. Total phosphorus ranges between 0.015 and 0.025% and fertility characteristics are generally similar to other northern Australian red earths (Day 1977, Isbell *et al.* 1976).

1.4.4 Vegetation

Rich and extensive mangrove communities line the alluvial soils on the lower reaches of Melville Island's waterways and a limited range of these communities have been described by Messell *et al.* (1979).

The upper reaches and springs of some creeks support evergreen rainforest. These communities are well developed on Melville Island relative to other regions of the Top End and are floristically related to semi-deciduous vine thicket (Russell-Smith and Dunlop 1987). The vine thicket communities occur where groundwater is absent or impermanent and are most common near the coast and on or below rocky slopes. These closed forests are currently being described by Russell-Smith (in prep.). Treeless vegetation includes small areas of floodplain comprised of grassland-sedgeland-saltmarsh complex. A unique community of grassy heath on deep well drained sand has largely been converted to *Pinus caribea* plantation at Yapilika and the remnants have been described by Wilson (1990).

While this array of vegetation types enriches the island's flora, the vast majority of its area is covered by eucalypt forest. Most of this forest is dominated by combinations of the evergreen species *Eucalyptus miniata, Eucalyptus tetrodonta* and *Eucalyptus nesophila* although some forests and woodlands are dominated by broadleaved semi-deciduous species such as *Eucalyptus latifolia, Eucalyptus confertiflora*

and *Eucalyptus oligantha*. A sparse layer of grass and herbs comprise the ground layer in the eucalypt forest hence justifying their description as savanna (Bourliere and Hadley 1983, Sanford and Isichei 1986).

1.4.5 Fire

Fire is almost an annual phenomena in Australia's tropical savanna. In the eucalypt forests on Melville Island, the first fires start burning when the grass in the ground layer is sufficiently dry around mid-June. Fire is a prominent feature of the landscape for the succeeding months and by the beginning of the following wet season most of the island's open forest and woodland have been burnt. The annual occurrence of fires and the sparse fuel loads ensures that fires typically burn cool and usually self extinguish at night. Fires are rarely hot enough to scorch tree crowns but do increase their intensity on windy days and late in the dry season when forest fuels are driest. Most fires are lit by people although lightning ignitions are common enough to ensure regular conflagration.

Aboriginal people were almost certainly the major source of ignition in the Australian landscape at the time of European arrival (Blainey 1975, Hallam 1975, Jones 1980, Kimber 1983). Haynes (1985) has produced a detailed ethnographic account of the burning practices of aboriginal people around Maningrida in northern Australia. He demonstrates that these people recognized that different biomes required specific fire regimes for optimum management of their resource. The recognition that fires burn hotter as the dry season progresses provides the main method of control. He records the burning of fire breaks early in the dry season to localize hot fires later in that season. Jones (1980) describes a strategy from coastal Arnhem Land that involves the burning of the peripheries of monsoon thickets early in the dry season to ensure that hot late dry season fires will not penetrate the relatively fire sensitive thicket vegetation.

There is evidence that fire was used by the Tiwi for specific purposes. The smoke lit by people when they were lost would indicate position to other people (Reid 1987, p 32). The lighting of fires under paperbarks

(*Melaleuca* spp.) was used to 'smoke out' magpie geese (Stocker 1966). On Karslake Peninsula, lines of people lit fires that were fanned by the prevailing southeasterly dry season winds. The fires drove game to the tip of the peninsula where they could be killed. This event had to be late enough in the dry season to ensure that the fire would carry effectively. Hart and Pilling (1960, p 41-2) describe a similar event and Bernard Tipungwuti described the events of his childhood when fire was used as a hunting tool (pers. comm. 1988). The lighting of rings of fire trapped game inside the circle. Dazed wallabies could be easily killed as they jumped the fire front to escape. Hart and Pilling (1960, p 42) refer to the lighting of fires to clear understorey vegetation. From my enquiries, 'cleaning up the country' seemed to be the most important reason for burning the bush and refers to several specific motivations. These reasons were reiterated to me many times by different people and make perfect sense to anyone who has been involved in dry season hunting trips. The first reason for burning is because the undergrowth that has accumulated over the previous year hinders walking. The requirement is particularly important when chasing game which requires the maximum agility of the hunter. Furthermore, the hunter can detect game more easily if the ground is clear and is less likely to lose track of animals during chase.

Traditionally it was usual for people to do the burning of their own country. Tiwi people who wished to burn outside their home territory would have to gain permission from an elder of that country (Goodale 1971, p 23-4). To a certain extent this traditional law is respected today.

Despite social restrictions governing the lighting of fires and the immediate motivations outlined above, there is little evidence in the literature nor did I find any during my visit that the Tiwi used fire to satisfy perceived requirements of the biota. The floodplain communities may be an exception and had specific attention because fire interrupted the nesting and feeding of magpie geese (Reid 1987, p 32). However, there is no evidence that fire was used to deliberately manipulate the environment for longterm ends in the way that Haynes (1985) and Jones (1980) have described for other tribes in northern Australia. The lack of a land management procedure directed towards satisfying perceived ecological requirements of specific

ecosystems may partly be a function of the monotony of the Melville Island eucalypt vegetation. However, monsoon thickets are prolific on the island and during my stay I was persistent in my enquiries regarding initiatives directed toward the requirements of this vegetation type. My pointed questions would be akin to "Did anyone ever burn around monsoon thickets early in the dry season so they would not be damaged by hot fires later in that season?" (as per Jones 1980). Responses ranged from "What would anyone want to do that for?" or more specifically "Haven't you realized that fires usually go out at the edge of thickets no matter when you burn and even if they don't the plants in the monsoon forest are fire resistant and resprout after fire in the same way as trees in the open forest?" It could be argued that detailed knowledge of fire management has been lost as hunting activities have declined. However, people of all ages still go hunting and it is difficult to imagine such knowledge disappearing without trace. Furthermore, anthropologists can uncover detailed information documented by earlier anthropologists about the original social fabric of Tiwi society despite the marriage of traditional Tiwi culture with modern western influences.

Tiwi people still burn the country they visit during the dry season although over the last two decades the forestry unit has systematically burnt the islands by using aerial incendiary devices.

CHAPTER 2 ENVIRONMENTAL CONTROL OF OPEN VEGETATION GRADIENTS ON WESTERN MELVILLE ISLAND

2.1 Introduction

There is general consensus that the cause of major gradients within the open vegetation in tropical Australia is variation in soil moisture regimes (Langkamp *et al.* 1981, Wilson and Bowman 1987). Specht *et al.* (1977) suggest that *Eucalyptus confertiflora-Eucalyptus cullenii* woodland is separated from *Eucalyptus tetrodonta* forest because the woodland occupies soils with limited water storage capacity and a tendency for waterlogging. Bowman and Minchin (1987) suggest that the accession of broadleaved species into the canopy occurs in situations where these species can exploit a water table that lies within the root zone during the dry season. There is a sound intuitive base for implicating soil moisture as a primary determinant of vegetation pattern given the strong seasonality of the rainfall and the need for studies that monitor moisture conditions over seasonal precipitation fluctuations has become obvious.

Soils bind water in specific ways depending on their physical properties (Gupta and Larson 1979, Williams *et al.* 1983). Water is held on the surfaces of clay particles by adsorption (Hillel 1971). Therefore, soils with high clay content generally have less available water than sandy soil. Soil matric potential is a measure of the suction required to remove water from the soil matrix. Determination of this value is an effective measure of the amount of water available to plants (Russell 1973, p 473). The present study determines soil matric potential and thereby circumvents assumptions relating easily collected environmental variables and real plant requirements.

Rice and Westoby (1985) have noted that structure and overstorey composition can vary without concomitant changes in understorey floristics. This discord is more likely in environments with low geomorphological variability (Kirkpatrick *et al.* 1987). Melville Island is clothed almost continuously by open eucalypt forest and woodland on lateritic substrates and is such an environment. Deep available soil

moisture may be influencing tree and shrub composition without affecting shallow rooted understorey species. It seems likely that these effects would be exacerbated in the monsoonal tropics where soils are drenched in the wet season and surface soils dry out thoroughly during the seven month drought. Thus, there is a need for studies that look at moisture availability through the soil profile (Medina and Silva 1990).

There is a school of plant geographers that have demonstrated that floristic pattern provides a very accurate reflection of environmental change. For this reason the floristic pattern of the open eucalypt forest on Melville island is presented. The chapter seeks to answer the following questions:

a) can floristic pattern be environmentally correlated?
b) can patterns of vegetation structure and overstorey composition be related to florisitic pattern?
c) Where florisitic patterns and overstorey patterns do not match, can the latter be related to sub-surface edaphic conditions?

The main body of the chapter seeks to quantify variations in seasonal soil moisture cycles through the soil profile and a range of environmental positions. This exercise aims to relate this variation to the structural and phytosociological patterns of savanna vegetation. The study also attempts to relate some soil chemistry data to vegetation characteristics across a range of savanna environments on Melville Island.

The vegetation gradients selected for study were chosen to encompass a range of structures and overstorey dominants, across a broad range of environmental conditions. If soil moisture relations are critical, then matching vegetation types should have similar patterns of moisture excess and deficiency regardless of differences in topographic and edaphic conditions. This study aims to test the assumption that interactions of different combinations of environmental situations can provide similar conditions for plants.

It is important to realise that plant access in various soil types may be inhibited. In the light of this fact, the distribution of roots through two contrasting soil profiles is examined.

The Top End distributions of some common tree species is provided from recent surveys. This provides an opportunity to compare the macro-climatic limits of these species with their environmental tolerances over local gradients.

2.2 Methods

2.2.1 Melville Island survey

Sampling was intended to cover the range of open forest and woodland (excepting dune vegetation) that cover the vast majority of the island. Ten x 10 m square quadrats were located along the roads of the western half of Melville Island but 100 steps orthogonal to road verges to avoid disturbance effects. Sampling was conducted during April and May 1986 when maximum plant species can be identified. All observable species were noted and the Bitterlich variable plot method was used to determine basal area and relative frequency of tree species using the centre of the quadrat as the sweep point (Mueller-Dombois and Ellenberg 1974). Undescribed species are held in the Darwin Herbarium. All quadrat data were entered into the program DECODA (previously ECOPAK, Minchin 1986). The data were ordinated using detrended correspondence analysis (DECORANA, Hill 1979a) which is probably the most robust of available ordinating techniques that do not demand an excessive computing resource (Brown *et al.* 1984). Twenty sites representative of the range of ordination values for the first, second and third axes were selected for the assessment of soil profiles and soil moisture content during September of the first field season (1986) when soils were approximating their driest. Holes were augered to 150 cm or the depth that their heaviness or rockiness allowed. A quantity of soil from 15, 45, 90 and 150 cm was weighed and then oven dried at 100° C for 24 hours. The dry soil was reweighed with and without gravel which was extracted with a 2 mm sieve. Profiles were described using the textural grades of McDonald *et al.* (1984); 1- sand, 2- loamy sand, 3- clayey sand,

4- sandy loam, 5- light sandy clay loam, 6- loam, 7- silt loam, 8- sandy clay loam, 9- clay loam, 10- silty clay loam, 11- sandy clay, 12- silty clay, 13- light clay, 14- light medium clay, 15- medium clay, 16- heavy clay.

In October 1986 six transects were established that traversed vegetation clines representing most of the major variation encountered during the vegetation survey or intimated by the ordination. Lines were scribed on aerial photographs that were orthogonal to vegetation boundaries. This line was transferred to the ground using a compass and measuring tape. Bearings and distances were noted and transects were marked by flagging trees with coloured tape. The transects ranged from 140 m to 2600 m in length.

Twenty x 20 m quadrats were located at varying distances along each transect such that distinct vegetation types were represented by at least one quadrat and ecotones were thoroughly sampled. The distance of each quadrat from the starting point was noted. From each quadrat the following size class data were collected. The species and diameter at breast height of all plants with >3 cm dbh were measured. The species and number of trees and tall shrubs in size classes of less than 15 cm high (H) and 15-50 cm H were recorded from five 2.5 x 2.5 m quadrats that were located within the larger quadrat using random numbers to define their coordinates. The same information was collected for size classes of 15-50 cm H and 50 cm H-<3 cm dbh from five 1 x 20 m strip quadrats located at right angles to the transect and every 4 m within the larger quadrat. During the optimum flowering period of the following year, all higher plant species were recorded from a 10 x 10 m quadrat located centrally within the larger quadrat.

The topography of the transects was surveyed using a dumpy level. Twenty-six sites were subjectively located along the transects for monitoring soil conditions. The soil information collected during the general survey was also recorded from these sites on the transects. However, the maximum depth was increased to 210 cm where possible, giving an additional sample at this depth. These soil measurements commenced in November 1986 with subsequent measurements in February, April, June and September of 1987. Soil

moisture information from March and October was also obtained for one of the transects (Section 3.2.1).

Soil chemistry

Soil samples from 15 cm depth were analysed from the 26 augered transect sites. Measurements of conductivity (1:5 solution using an electrical conductivity meter), pH (1:5 solution using a pH meter), nitrogen (available ppm, extracted in potassium chloride)(CSIRO 1982), phosphorus (available ppm, Olsen method, extracted in sodium bicarbonate at pH 8.5 for 16 hrs), potassium (available ppm, extracted with ammonium acetate, Juo *et al.* 1976), calcium (available ppm, extracted with ammonium acetate, Juo *et al.* 1976) and magnesium (available ppm, extracted with ammonium acetate, Juo *et al.* 1976) were determined.

Soil physical characteristics

A range of soils encountered during the survey (represented by 44 soil samples) were collected for analysis of physical characteristics. Particle size analysis was performed using the methods of Coventry and Fett (1979). Moisture characteristic curves were determined by the method of McIntyre (1974) at 0.1, 1.3, 5 and 15 bars.

The moisture characteristic curves were classified subjectively by similarity of shape using a light table. The residuals from regressions between combinations of field texture, coarse sand, fine sand, silt and clay and gravimetric moisture content at various values of Ψ were nearly always smallest for field texture values alone. The strongest correlation was between field texture and moisture values at 5 bars ($r = 0.784$, $P = <0.001$). This result was also found by Williams *et al.* (1983) who suggested that field texture is the single most useful measure of a soil's physical condition because it summarizes a range of other properties. Any of the classificatory groups whose mean field texture scores were within one unit of another group were amalgamated. This procedure established five groups from the 44 matric potential curves. The mean field texture scores (5.4, 7.5, 9.6, 10, 14) of these soil groups cover the range of texture classes encountered.

Regressions were performed between $\log_n$ gravimetric soil moisture (θ) and $\log_n$ matric potential (Ψ) for each of the five groups (Williams *et al.* 1983). The resulting functions were derived in an attempt to provide a single moisture characteristic from field texture and gravimetric moisture content that has some ecological reality for plants (Fig. 2.3). The functions were used to provide values of Ψ for all soils through their annual wetting cycle.

Multivariate and statistical treatment

DECODA contains the non-metric multidimensional scaling technique KYST that has been demonstrated to be the most robust of available ordinating techniques (Minchin 1987). This technique demands a considerable computing resource that is prohibitive for most students of ecology and was used here in two, three and four dimensions with ten starts, one of which had a starting configuration defined by its DECORANA scores. Following ordination of the complete Melville Island data set the procedure was repeated with only forest plots included. Presence-absence floristic data were classified using the program TWINSPAN (Hill 1979b) a polythetic divisive technique based on the splitting of successive ordinations that overcomes many of the major foibles of agglomerative or monothetic techniques (Gauch and Whittaker 1981).

Correlations between basal areas of woody species, ordination scores, texture scores, mean gravel content, gravimetric moisture content and Ψ values for all depths and measuring times were determined. The direction and strength of the vectors that best describe the relationship of environmental variables through the three dimensional ordination space were determined by rotational correlation analysis. ANOVA (following $\log_n(x+1)$ transformation where appropriate) by TWINSPAN group of these environmental variables and the distance of quadrats to the nearest monsoon forest was performed.

For each augered site, a drought index was calculated by summing the number of weeks that Ψ at each soil depth was greater than 4.5 bars. These values were extrapolated from graphs of seasonal fluctuations in

Ψ (Figs. 2.7-12). These values were multiplied by the depth of soil they would represent if they were mid-points for depth classes down to 2 m (15 cm covers a depth of 30 cm, 45 cm covers 37.5 cm, 90 cm covers 52.5 cm and 150 cm covers 80 cm). These products were summed to give a drought index at each site. The index assumes that water is equally accessible from all depths down to two metres. A waterlogging index was obtained by counting the number of weeks that each soil depth was inundated. The occurrence of woody species as canopy members was graphed on a direct ordination space with droughtiness and waterlogging as the axes. This was divided into 4 cells and a chi-squared test performed on a contingency table made up of the presence and absence of tree species in well drained and waterlogged halves of the ordination space. The same test was performed on the droughty and non-droughty halves of the space.

2.2.2 Root excavation

Examination of tree root systems was carried out in November 1988. A trench was dug in a forest dominated by *Eucalyptus miniata* (site 16, Fig. 2.9) and another trench in semi-deciduous low forest dominated by *Eucalyptus latifolia*. (site 19, Fig. 2.9). Exploratory digging revealed negligible tree roots below the surface soil at both sites. Further root exploration involved placing trenches adjacent to two nearby trees in order to reveal the extent of tap roots. Trenches were dug with a backhoe to a length of 4.5 m and a depth of 1.4 m. The first trench was positioned adjacent to *Eucalyptus miniata* (26 cm dbh) and *Eucalyptus nesophila* (13 cm dbh) individuals and the second adjacent to *Eucalyptus latifolia* (24 cm dbh) and *Terminalia ferdinandiana* (9 cm dbh) trees. The number of tree roots in size classes, <1 mm, 1-10 mm and >10 mm were scored in 27 50 cm long x 20 cm deep cells to a depth of 60 cm and then in 18 50 x 40 cm cells to a depth of 140 cm at each site.

2.3 Results

2.3.1 Indirect gradient analysis of Melville Island vegetation patterns

Three hundred and nineteen species were recorded during the Melville Island survey and the ß-diversity of the data set was 3.1 half changes as measured by DECORANA's first axis. This reflects considerable variation in the apparently monotonous open forest and woodland formations. Five groups with ecological reality can be recognised from the TWINSPAN classification (Table 2.1). The first division splits the communities occurring on thin gravelly topsoils over heavy clays (group 1) from other communities (group 0). Interestingly the two sub-groups that comprise group 1 occupy opposite extremes of a drainage gradient. The first sub-division of this group (10) is dominated by *Melaleuca viridiflora* and occurs on low-lying flat areas with free water at surface level for the five month wet season. The other sub-division (11) is dominated by *Eucalyptus bleeseri* and occurs on uplands and ridges on the driest substrates. The communality of the two groups is a function of their understoreys. They both share the faithfully dominant annual grass *Eriachne burkitti* and the understorey graminoid *Rhynchospora heterochaeta.* A whole suite of species are almost totally confined to group 10, the most common of which are the herbs *Burmannia juncea, Cartonema parvifolia, Lindernia scapigera* and the graminoid, *Fimbristylis* sp. The pea *Tephrosia elliptica,* the graminoid *Fimbristylis simplex* and the shrub *Calytirx acaeta* are faithful and frequent in group 11. At the other extreme of the first ordination, group 00 is characterised by a suite of annual grasses, *Eriachne obtusa, Eriachne squarrosa, Eragrostis cummingii* and *Digitaria gibbosa,* and the wattles *Acacia difficilis, Acacia gonocarpa* and *Acacia oncinocarpa.* These *Acacia* species replace other species in the same genus that are common in the open forest comprising other groups. Group 00 always occurs on deep sandy loams and can include *Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta* forest or *Eucalyptus polycarpa* woodland.

Plots in group 01 were situated in the forest that cover most of the island. These forests and the forest plots of group 00 are structurally uniform and dominated by admixtures of *Eucalyptus miniata,*

Table 2.1 Percentage frequency according to TWINSPAN group. Only species occurring with a frequency of more than 25% in any one group are included.

PLANT SPECIES	TWINSPAN GROUP				
	00	010	011	10	11
Digitaria gibbosa	66.7	-	-	-	-
Gonocarpus implexus	66.7	1.5	-	-	-
Acacia gonocarpa	66.7	2.3	-	-	-
Acacia oncinocarpa	55.6	6.8	-	-	-
Eragrostis cumingii	66.7	17.4	14.3	-	-
Eriachne squarrosa	100.0	18.2	14.3	-	-
Setaria apiculata	55.6	14.4	19.1	-	-
Pachynema complanatum	11.1	48.5	-	-	-
Acacia difficilis	77.8	3.8	-	4.6	-
Brachiaria holosericea	77.8	9.9	4.8	4.6	-
Persoonia falcata	55.6	63.6	23.8	4.6	-
Sauropus dittasoides	-	32.6	-	-	-
Alloteropsis semialata	-	47.7	28.6	4.6	-
Murdannia gigantea	-	37.1	28.6	-	-
Vigna lanceolata	-	30.3	28.6	-	-
Erythrophleum chlorostachys	-	43.2	52.4	4.6	-
Eucalyptus miniata	11.1	62.1	28.6	-	-
Kailarsenia suffruticosa	-	35.6	19.1	4.6	-
Planchonella pohlmaniana	11.1	17.4	28.6	-	-
Sauropus brunonis	-	31.1	19.1	-	-
Thaumastochloa major	22.2	48.5	23.8	-	-
Eucalyptus tetrodonta	22.2	50.8	19.1	-	-
Desmodium sp. 'clavitricha'	11.1	49.2	42.9	22.7	-
Mitrasacme sp. CRD 3971	-	28.8	-	-	33.3
Brachychiton paradoxus	-	15.2	28.6	-	-
Chrysopogon fallax	-	47.0	33.3	9.1	-
Crotolaria linifolia	-	25.8	9.5	4.6	-
Galactia tenuiflora	-	27.3	9.5	9.1	-
Acacia leptocarpa	-	18.94	33.3	4.6	-
Ampelocissus acetosa	-	24.2	61.9	13.6	-
Flemingia parviflora	-	63.6	63.7	18.2	-
Polygala orbicularis	-	31.8	42.9	9.1	-
Spermacoce australiana	-	22.0	33.3	9.1	-
Acacia latescens	66.7	18.2	4.8	4.6	-
Cheilanthes tenuiflora	-	31.1	19.1	9.1	-
Eulalia mackinlayi	-	37.1	23.8	9.1	6.7
Phyllanthus revoluta	11.1	9.1	-	-	33.3
Buchanania obovata	11.1	59.9	23.8	40.9	-
Scleria brownii	-	12.1	33.3	9.1	-
Acacia aulacocarpa	-	69.7	57.1	40.9	-
Plachonia careya	11.1	71.2	90.5	40.9	-
Rottboellia formosa	-	12.9	52.4	9.1	-
Breynia cernua	-	4.6	85.7	-	-
Coelorachis rotboellioides	-	8.3	33.3	-	-
Cycas armstrongii	-	36.4	57.1	-	-
Dioscorea transversa	-	0.8	28.6	-	-
Grewia multiflora	-	0.7	57.1	-	-
Smilax australis	-	3.0	52.4	-	-

Table 2.1 (continued).

Themeda arguens	-	3.0	52.4	-	-
Eriachne avenacea	11.1	63.6	-	18.2	100.0
Calogyne holtzeana	-	8.3	4.8	9.1	33.3
Eucalyptus bleeseri	-	13.6	4.8	-	100.0
Eucalyptus nesophila	33.3	45.5	23.8	36.4	-
Grevillea decurrens	33.3	28.0	4.8	4.6	100.0
Hibbertia cistifolia	44.4	75.0	33.3	50.0	33.3
Livistona humilis	22.2	53.0	28.6	63.6	-
Phyllanthus simplex	-	23.5	23.8	27.3	-
Sauropus glaucus	11.1	32.6	-	36.4	-
Eriachne obtusa	100.0	3.8	-	-	66.7
Grevillea pteridifolia	55.6	19.7	4.8	18.2	-
Mitrasacme elata	100.0	18.9	4.8	22.7	-
Shizachyrium fragile	88.9	20.5	19.1	27.3	-
Curcuma australasica	-	-	33.3	4.6	-
Hibiscus meraukensis	-	2.3	28.6	4.6	-
Ipomoea gracilis	-	2.3	38.1	9.1	-
Sorghum plumosum	55.6	21.2	9.5	4.6	-
Spermacoce sp. JRS & DL 2430	77.8	57.6	19.1	22.7	-
Alphitonia excelsa	33.3	39.4	38.1	13.6	-
Eriachne triseta	100.0	62.9	66.7	22.7	-
Terminalia ferdinandiana	11.1	36.4	28.6	63.6	-
Drosera petiolaris	11.1	21.2	-	36.4	66.7
Gardenia megasperma	-	9.9	4.8	36.4	-
Wrightia saligna	11.1	9.1	-	27.3	-
Xyris complanatus	-	3.8	-	4.6	66.7
Petalostigma quadriloculare	-	6.8	-	-	33.3
Scleria sphacelata	-	4.6	-	4.6	33.3
Cassytha filiformis	-	1.5	-	-	33.3
Tacca leontopetaloides	-	3.0	42.9	13.6	-
Lophostemon lactifluus	-	5.3	14.3	81.8	-
Pandanus spiralis	-	15.9	38.1	50.0	-
Calytrix exstipulata	44.4	2.3	-	9.1	-
Pseudopogonatherum contortus	66.7	47.0	38.1	95.5	-
Burmannia juncea	-	-	-	27.3	-
Cartonema parviflora	-	0.8	-	40.9	-
Fimbristylis acuminata	-	-	-	36.4	-
Fimbristylis sp.	-	-	-	40.9	-
Ischaemum decumbens	-	0.8	4.8	50.0	-
Lindernia scapigera	-	0.8	4.8	50.0	-
Melaleuca viridiflora	-	3.0	14.3	81.8	-
Sacciolepis indica	-	0.8	-	36.4	-
Spermacoce brevifolia	11.1	0.8	4.8	68.2	-
Syzigium eucalyptoides	-	0.8	-	31.8	-
Eucalyptus grandifolia	-	1.5	9.5	27.3	-
Mitrasacme arnhemicus	-	3.8	14.3	77.3	-
Petalostigma pubescens	-	21.2	14.3	27.3	66.7
Eriachne burkitti	-	14.4	19.1	95.5	100.0
Rhyncospera sp.	-	3.0	4.8	72.7	100.0
Goodenia leiosperma	-	10.6	9.5	45.5	100.0
Calytrix achaeata	-	-	-	-	66.7
Fimbristylis simplex	-	5.3	-	18.2	100.0
Tephrosia elliptica	-	0.8	-	-	100.0
No. of quadrats	9	132	21	22	3

Eucalyptus nesophila and *Eucalyptus tetrodonta* any of which occasionally form pure stands. The midstorey is extremely sparse and most commonly occupied by the small trees *Acacia aulacocarpa, Acacia leptocarpa, Acacia latescens, Grevillea decurrens* and *Terminalia ferdinandiana*. The sparse grassy ground layer is dominated by combinations of the grasses *Alloteropsis semialata, Eriachne avenacea, Chrysopogon fallax, Eulalia mackinlayi, Sorghum plumosum, Eriachne triseta* and *Pseudopogonatherum contortum,* whose growth and flowering are staggered from September to April respectively. The small trees mentioned above that occasionally make it to the midstorey and *Buchanania obovata, Planchonia careya, Brachychiton paradoxum* and *Persoonia falcata* that reach the midstorey more rarely are extremely abundant in the ground layer. They occur in this stratum with the taller tree species *Eucalyptus miniata, Eucalyptus nesophila, Eucalyptus tetrodonta, Eucalyptus confertiflora, Erythrophleum chlorostachys* and *Alphitonia excelsa* as woody sprouts from lignotubers and root suckers. The palm *Livistona humilis* and the cycad *Cycas armstrongii* occur in all size classes up to 8 m and are locally common throughout the open forest of the island. A variety of other species also occur in the ground layer and are listed here with their frequency of occurrence in the 131 quadrats of group 010: the annual grasses, *Thaumastachloa major, Schizachyrium fragile,* the annual herbs *Spermacoce* sp. JRS and DL 2430, *Sauropus brunonis, Mitrasacme* sp. CRD 3971, the perennial herbs *Desmodium* sp. 'clavitricha', *Sauropus glaucus, Murdannia gigantea, Gardenia suffruticosa, Sauropus dittasoides, Polygala orbicularis, Buchnera linearis, Crotolaria linifolia, Phyllanthus simplex,* the trailers *Flemingia parvifolia, Galactia tenuifolia,* the sub-shrubs *Hibbertia cistifolia, Pachynema complanatus* and the fern *Cheilanthes tenuifolia.*

Only one sub-group of the large eucalypt forest group 01 can be environmentally correlated. This is a section of the forest cline (011) that is characterised by the presence of the low shrubs *Breynia cernua* and *Grewia multiflora,* the vine *Smilax australis* and the grass *Themeda arguens,* and the absence of *Eriachne avenacea, Sauropus dittasoides, Sauropus glaucus, Mitrasacme* sp. CRD 3971, *Drosera petiolaris and Pachynema complanatus,* all of which are very common in 010. These plots are statistically more proximal to monsoon forest

than the plots comprising group 010 (ANOVA; $P<0.001$). They occur on a variety of substrates from deep sandy loams of flat landscapes to steep rocky banks and moderate to heavy soils that suffer poor drainage. The sites of this group on heavy soils are dominated by deciduous eucalypts. All of the sites from the eucalypt forest of Karslake Peninsula, that Stocker (1971) suggests was a monsoon forest in the recent past, are included in group 010. It seems that the environmental reason for the existence of monsoon forest determines the second axis of the ordination. Sites with affinities to monsoon forest comprise the lower portion of the ordination space and includes a cluster of sites in anomalous shrubby low woodland dominated by mixtures of *Melaleuca viridiflora* and deciduous eucalypts with open shrubby understoreys dominated by monsoon forest species. The latter community is probably related to the mixed forests described by Bowman and Dunlop (1986) and are extensive around the southern part of Melville Island at Cape Gambier.

KYST requires that the dimensionality of the ordination be predetermined. A three dimensional solution seemed marginally more desirable than solutions in lower or higher dimensions, following examination of the relationship between stress and the number of dimensions, the compositional trends of sites in other dimensions (see Bowman and Minchin 1987) and the fact that axis 3 could be environmentally correlated (Appendix 1 and 2). Appendix 1 presents the significance of correlations between selected biotic and environmental variables for the entire data set and Appendix 2 presents the same for forests only. The direction of vectors through the three dimensional ordination space that have the maximum correlation with environmental features are presented in Fig. 2.1. The transition from sand to clay at 45 and 90 cm occurs in the opposite direction to decreasing availability of wet season moisture. The tendency for higher moisture status as soils get heavier reflects the frequent presence of clay soils in run on situations. Variation in dry season soil moisture measurements tend to be orthogonal to the soil texture gradient which suggests these environmental measures are poorly related. It is interesting that the micronutrients calcium and magnesium show stronger relationships with ordination scores than

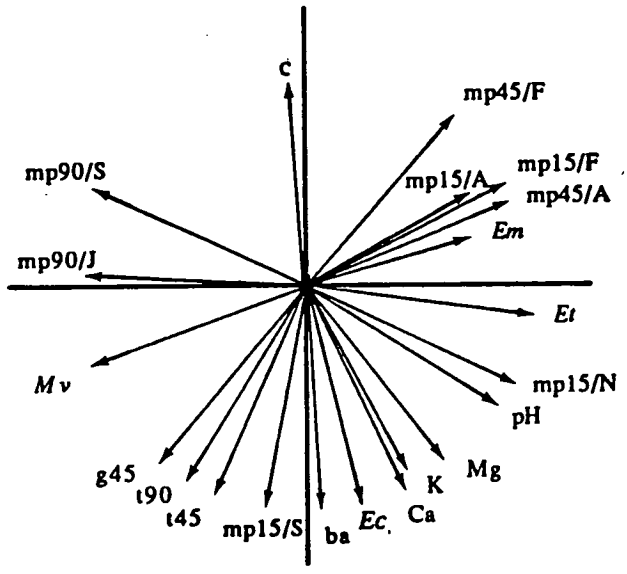


Figure 2.1 Vectors of environmental and vegetation variables through the three dimension KYST ordination space. The vectors represent the line of best fit and point towards the direction of highest values. The shorter the vector the more its directionality is in the third dimension. Only those variables that were significantly related at $P<0.01$ are included. The codes and the correlation coefficients of the vectors are as follows: *Ec Erythrophleum chlorostachys*- 0.30*, *Em Eucalyptus miniata*- 0.47**, *Et Eucalyptus tetrodonta*- 0.50**, *Mv Melaleuca viridiflora*- 0.58**, ba basal area- 0.34**, g45 gravel 45 cm(%)- 0.45*, t45 texture 45 cm- 0.59*, t90 texture 90 cm- 0.74**, Ca available calcium- 0.74**, K available potassium- 0.64**, Mg available Magnesium- 0.70**, pH- 0.86**, c conductivity- 0.55*, mp15/N $\log_n|\Psi|$ 15 cm November- 0.58*, mp15/F $\log_n|\Psi|$ 15 cm February- 0.65**, mp45/F $\log_n|\Psi|$ 45 cm February- 0.60*, mp15/A $\log_n|\Psi|$ 15 cm April- 0.68**, mp45/A $\log_n|\Psi|$ 45 cm April- 0.59*, mp90/J $\log_n|\Psi|$ 90 cm June- 0.58*, mp15/S $\log_n|\Psi|$ 15 cm September- 0.44*, mp90/S $\log_n|\Psi|$ 90 cm September- 0.48*; where * $P<0.01$, ** $P<0.001$. Tested variables that were not significant at $P<0.01$ are *Eucalyptus confertiflora, Eucalyptus nesophila, Terminalia ferdinandiana,* texture 15 cm, gravel 15 cm, available nitrogen, available phosphorus, $\log_n|\Psi|$ 45 cm November, $\log_n|\Psi|$ 90 cm November, $\log_n|\Psi|$ 90 cm February, $\log_n|\Psi|$ 90 cm April, $\log_n|\Psi|$ 15 cm June, $\log_n|\Psi|$ 45 cm June, $\log_n|\Psi|$ 45 cm September.

the macronutrients nitrogen and phosphorus. The former two elements and potassium vary in the same direction through the ordination space and the abundance of *Erythrophleum chlorostachys* shows a similar trend (Fig. 2.1). Correlations between the abundance of major tree species and environmental factors within the forest sub-set are scarce (Appendix 2).

Fig. 2.2 traces the floristic variation of the transects (Figs, 2.6-2.11) across the ordination space. The *Melaleuca viridiflora* woodland at the beginning of transect 2 (Fig. 2.7) occupies one extreme of axis one and are clearly separated from the forests that complete this transect (Fig 2.2). The floristic gradient of transect 4 (Fig. 2.9) is spread across axis two while transect 6 (Fig. 2.11) shows a diagonal trend across the first two dimensions of the ordination space (Fig. 2.2). At least some sections of these three transects show unidirectional trends across the ordination space but this relationship is not evident for transects 1, 3 and 5 (Figs. 2.6, 2.8 and 2.10 respectively). This conclusion is derived following examination of transect variation in the third dimension of the ordination space. Thus, overstorey changes can occur without complementary changes in understorey and particular tree species can dominate on a variety of substrates, topographic positions and with a range of associated understoreys.

2.3.2 Direct gradient analysis of Melville Island vegetation patterns

The moisture characteristic curves of the soil textural groups are presented in Fig. 2.3 and their predictive utility is indicated by Fig. 2.4. The limitations of field texture as a measure of pedality, grade of structure (Butler 1955) and size class composition, all of which affect moisture characteristic curves (Williams *et al.* 1983) probably account for most of the residuals in Fig. 2.4. The models support findings in the literature that moisture is progressively more difficult to extract as soils get heavier (Prebble 1970, Gupta and Larson 1979, Williams *et al.* 1983, Fig. 2.4), which suggests they are a useful approximation of "reality".

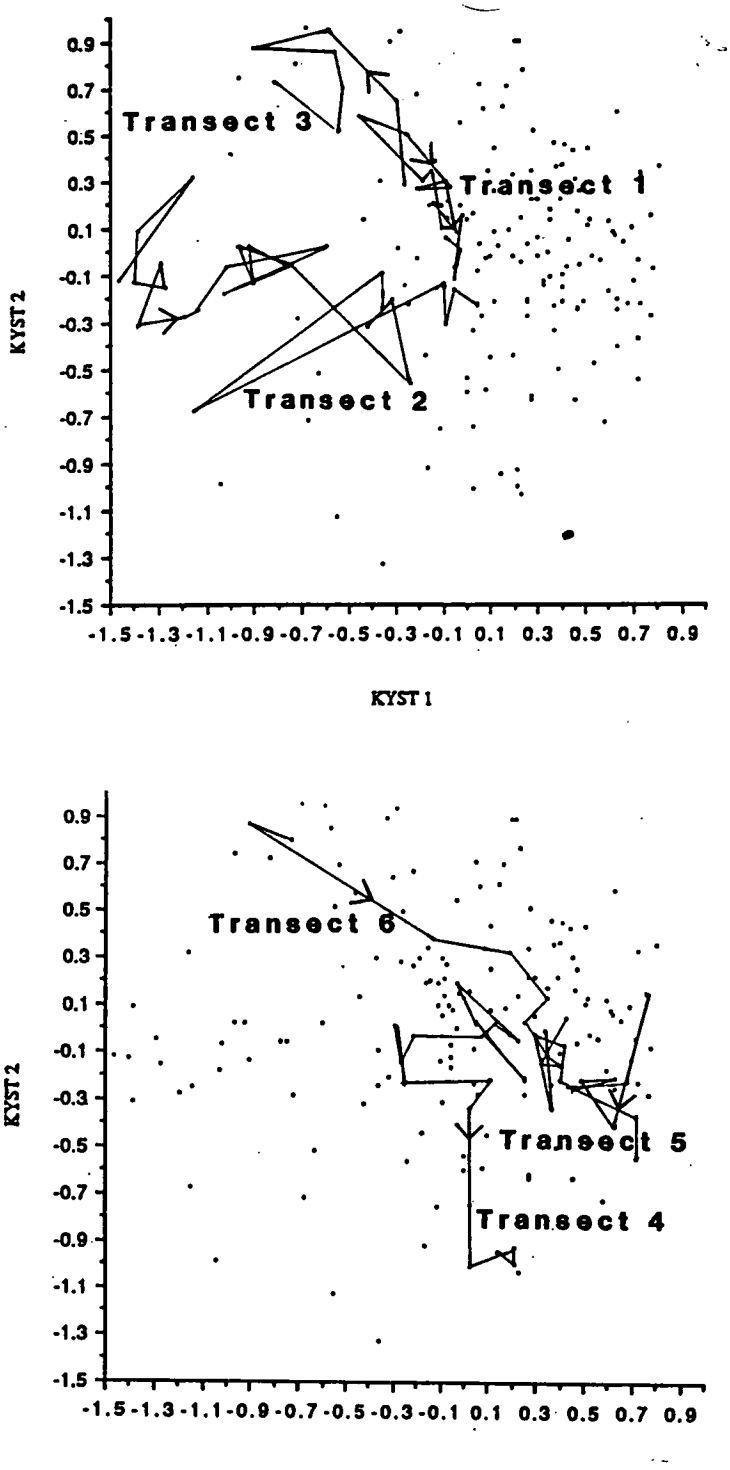


Figure 2.2 Quadrats marked on the first two dimensions of the three dimensional KYST ordination of the Melville Island data set. The position and direction of transects 1-6 as they are represented from left to right on Figs. 2.6-11 is indicated.

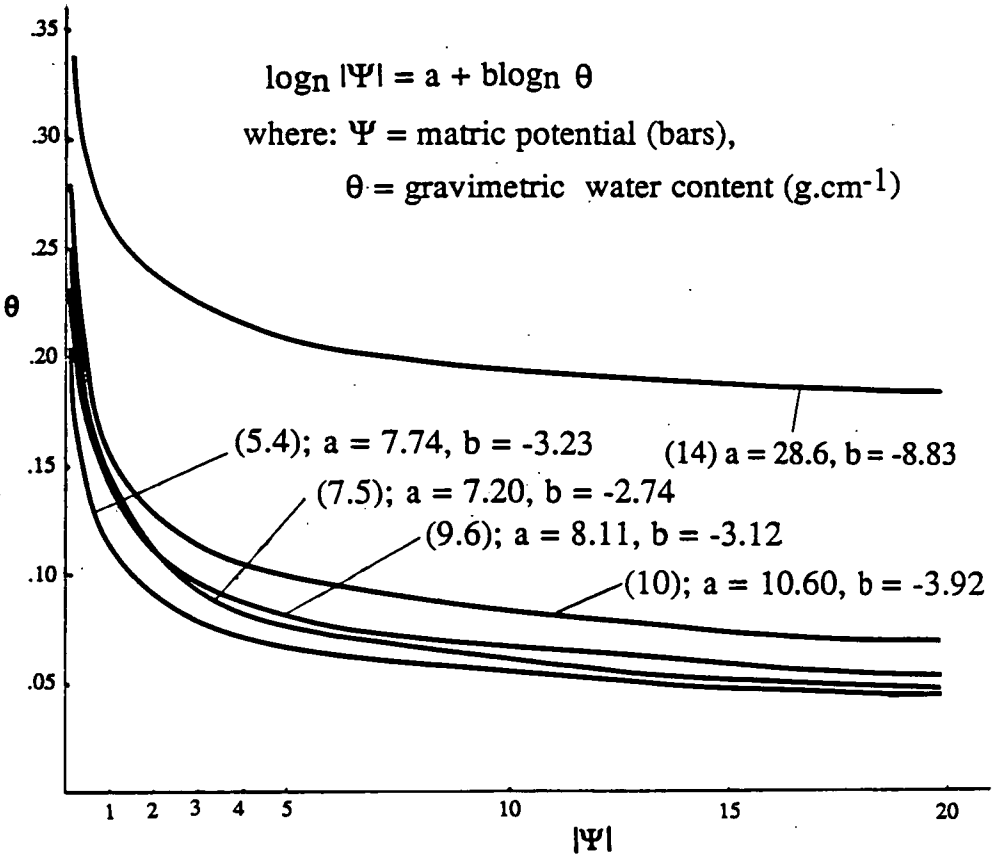


Figure 2.3 Moisture characteristic curves for five soil textural grades. Textural scores are mean values for the classes of McDonald *et al.* 1984.

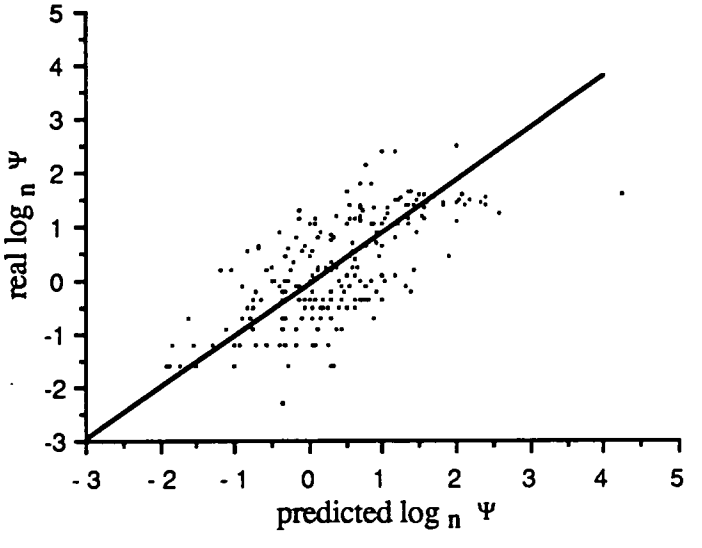


Figure 2.4 Predictive accuracy of derived matric potential (Ψ) values.

The rainfall for the sampling period was above average (Fig. 2.5). The vegetation and soil profile, annual moisture availability cycles and the abundances of woody species along transects 1-6 are presented in Figs. 2.6-2.11. Before discussing the relationships expressed in these figures the special problems involved with sampling soils that include significant quantities of gravel need to be discussed. Any particular sample can have varying proportions of gravel that are unable to absorb water (Fensham unpublished data). The soil around these inclusions has a greater proportion of moisture than areas of the sub-surface space from the same depth with lower proportions of gravel. Fluctuations in Ψ that contradict the seasonal precipitation cycle in some rocky soils result from greater concentrations of moisture in the soil as the proportion of rock increases. In rocky soils, the proportion of rock varies and this results in variable measures of moisture content in proximal samples. For example, Ψ at 45 cm from site 1 (Fig. 2.6) has lower moisture levels in June (Ψ is higher) than September despite negligible rain between these periods (Fig. 2.5). In this instance, the September sample had over 30% gravel while the June sample had 10%. This discrepancy in gravel content accounts for the incongruous moisture contents of the gravel free soil portion at the two times. The moisture content of the total sample (including gravel) is higher in June than September as would be expected following 3 months of evapotranspiration.

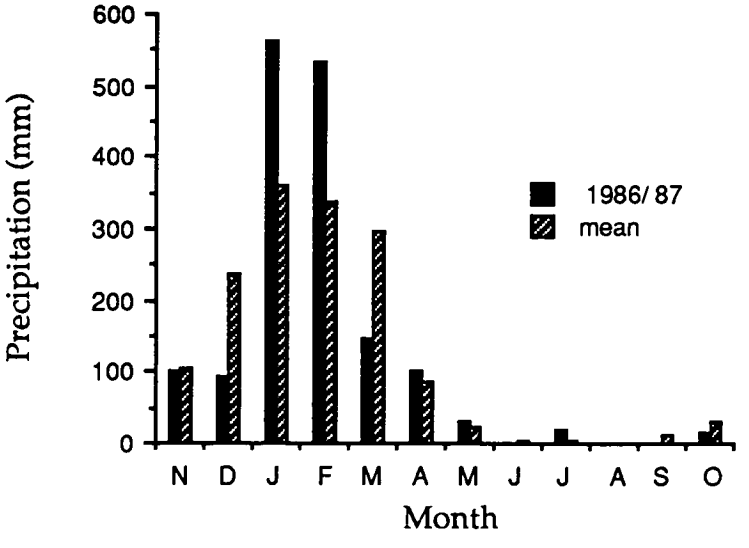


Figure 2.5 Mean annual rainfall and 1986/87 rainfall at Nguiu, Bathurst island (Bureau of Meteorology, Darwin).

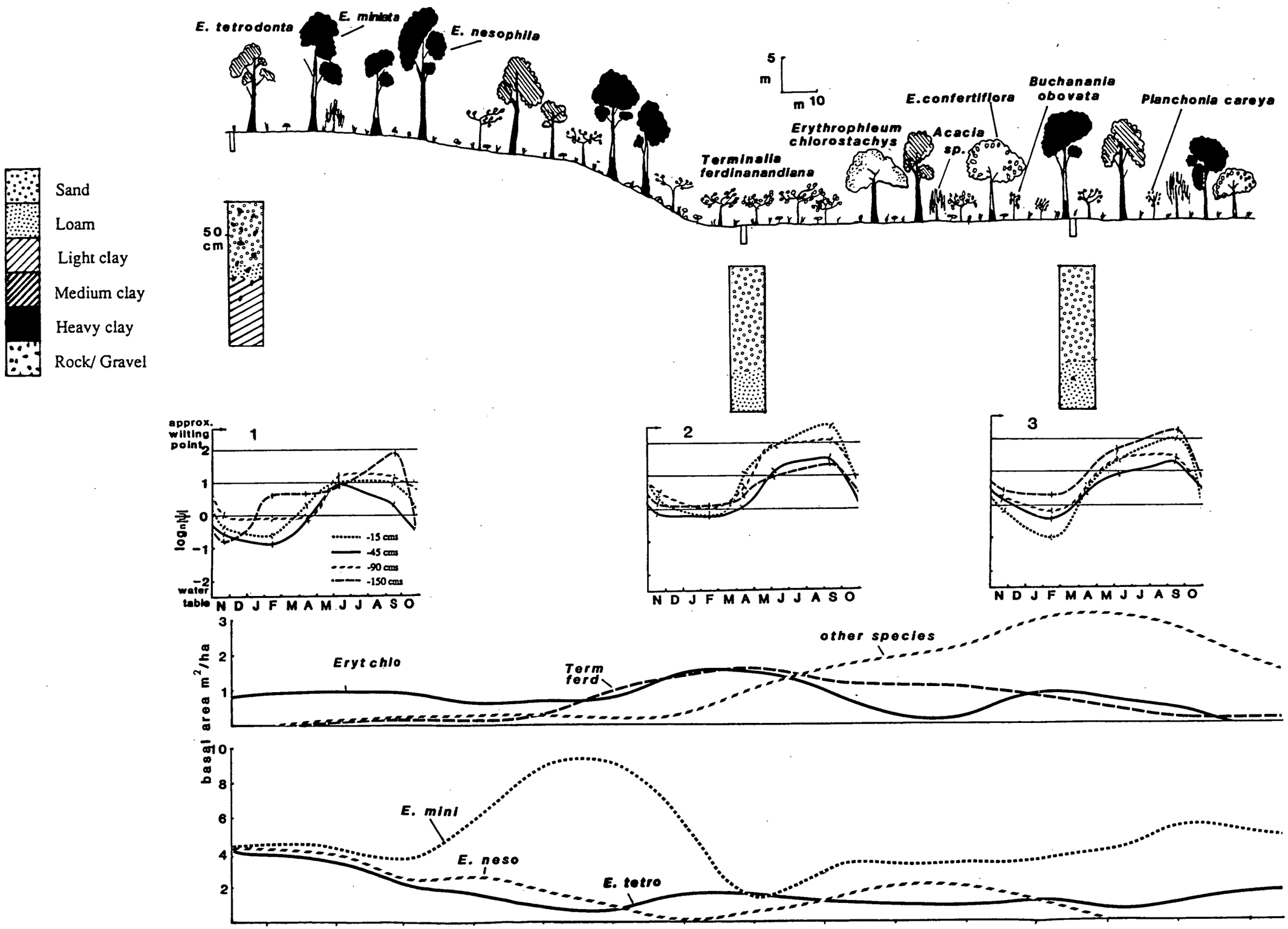


Figure 2.6 Transect 1. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. Approximate location of first quadrat Melville 805 115. Approximate direction 280^0.

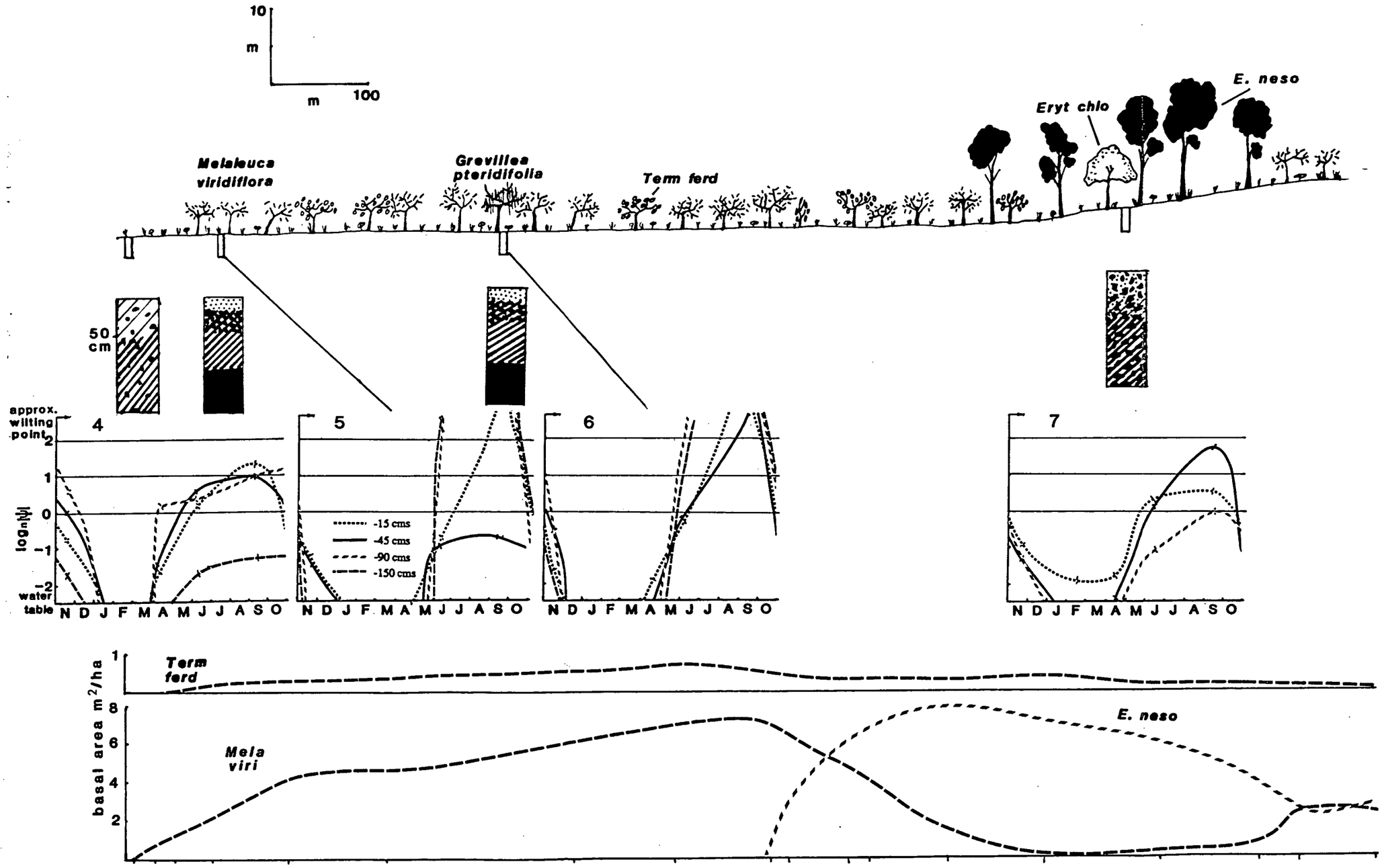


Figure 2.7 Transect 2. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. The key to the soil profile diagrams are presented on Fig. 2.6. Approximate location of the first quadrat Melville 843 263. Approximate direction 340^0.

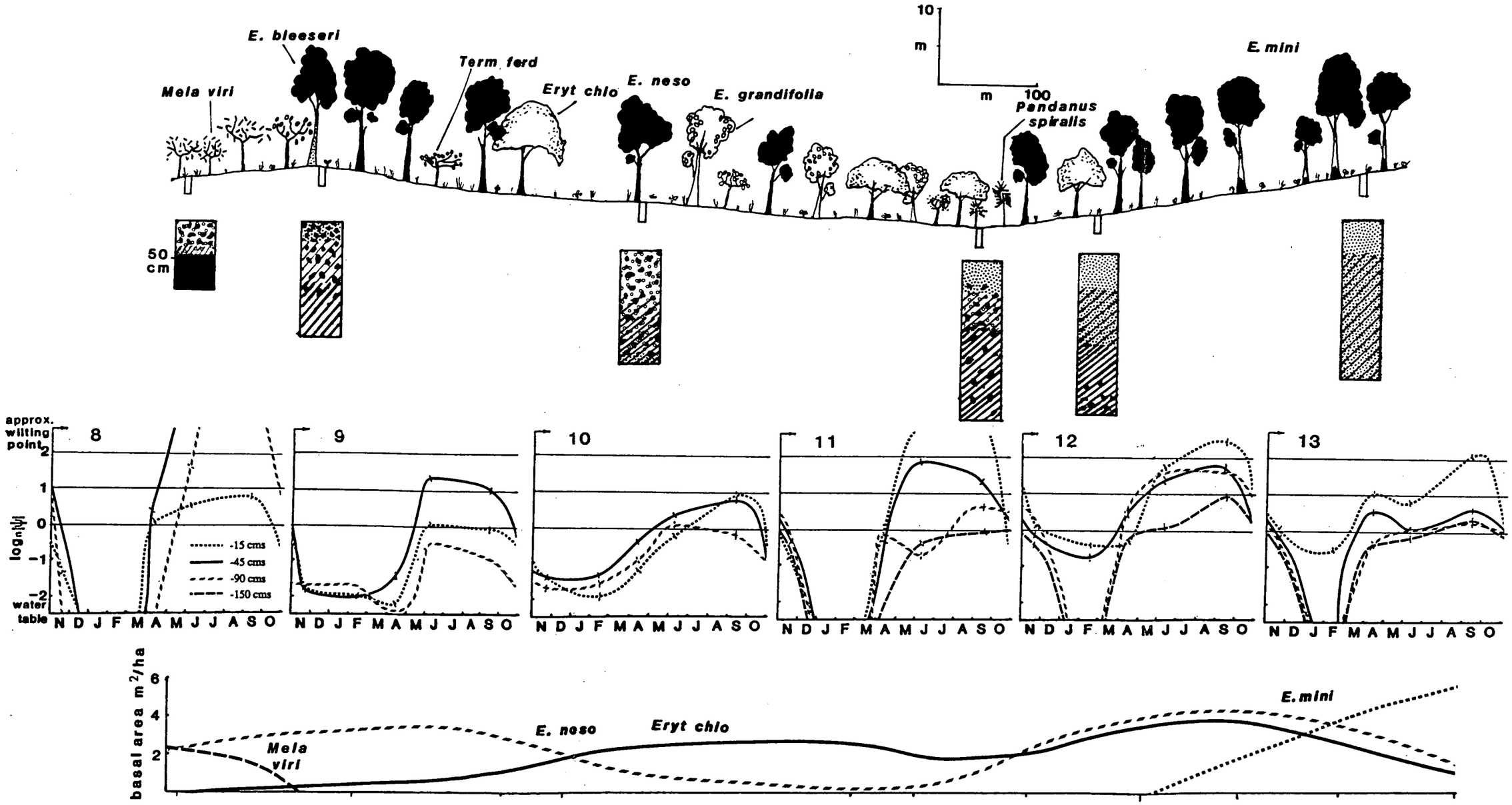


Figure 2.7 continued

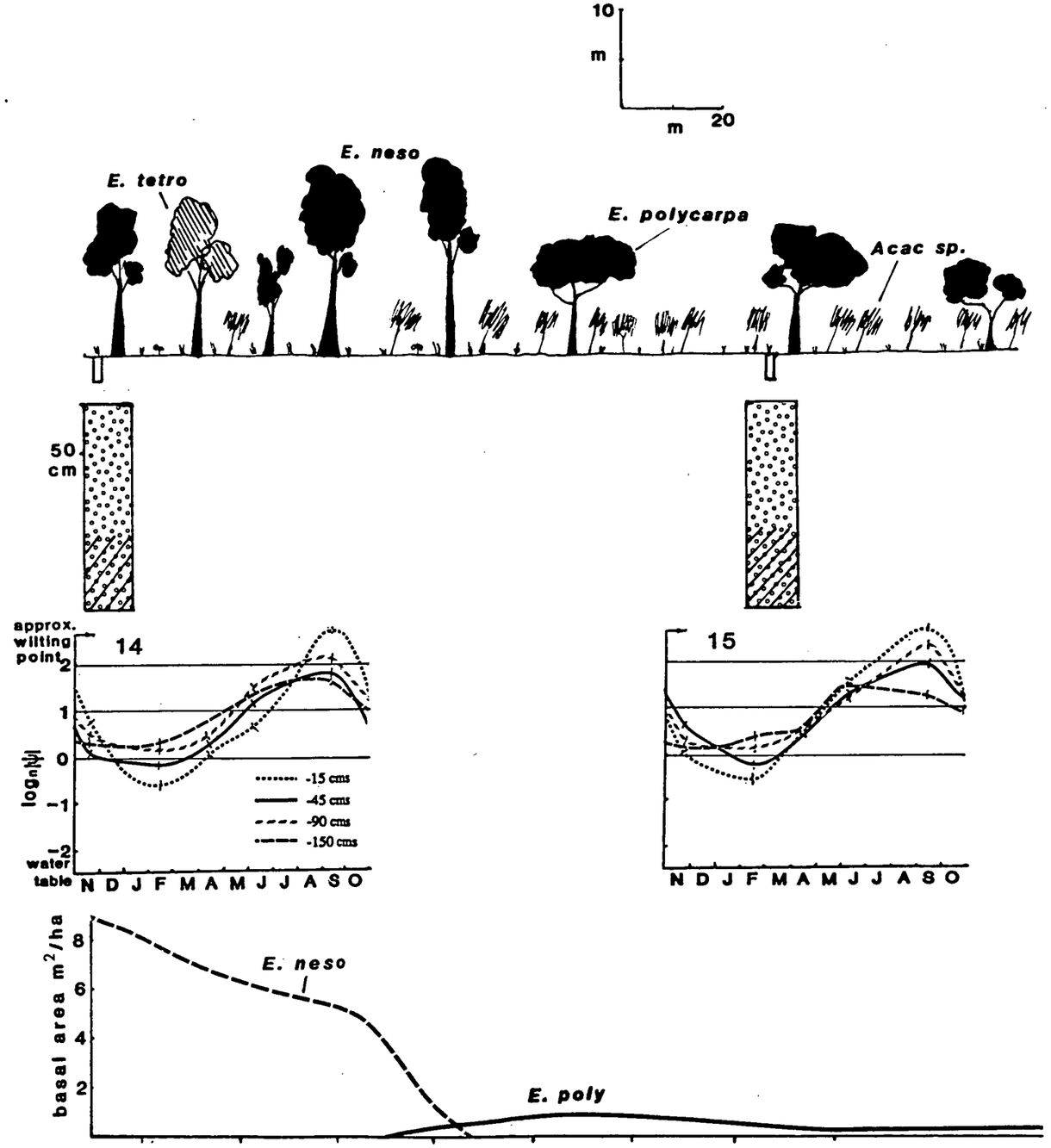
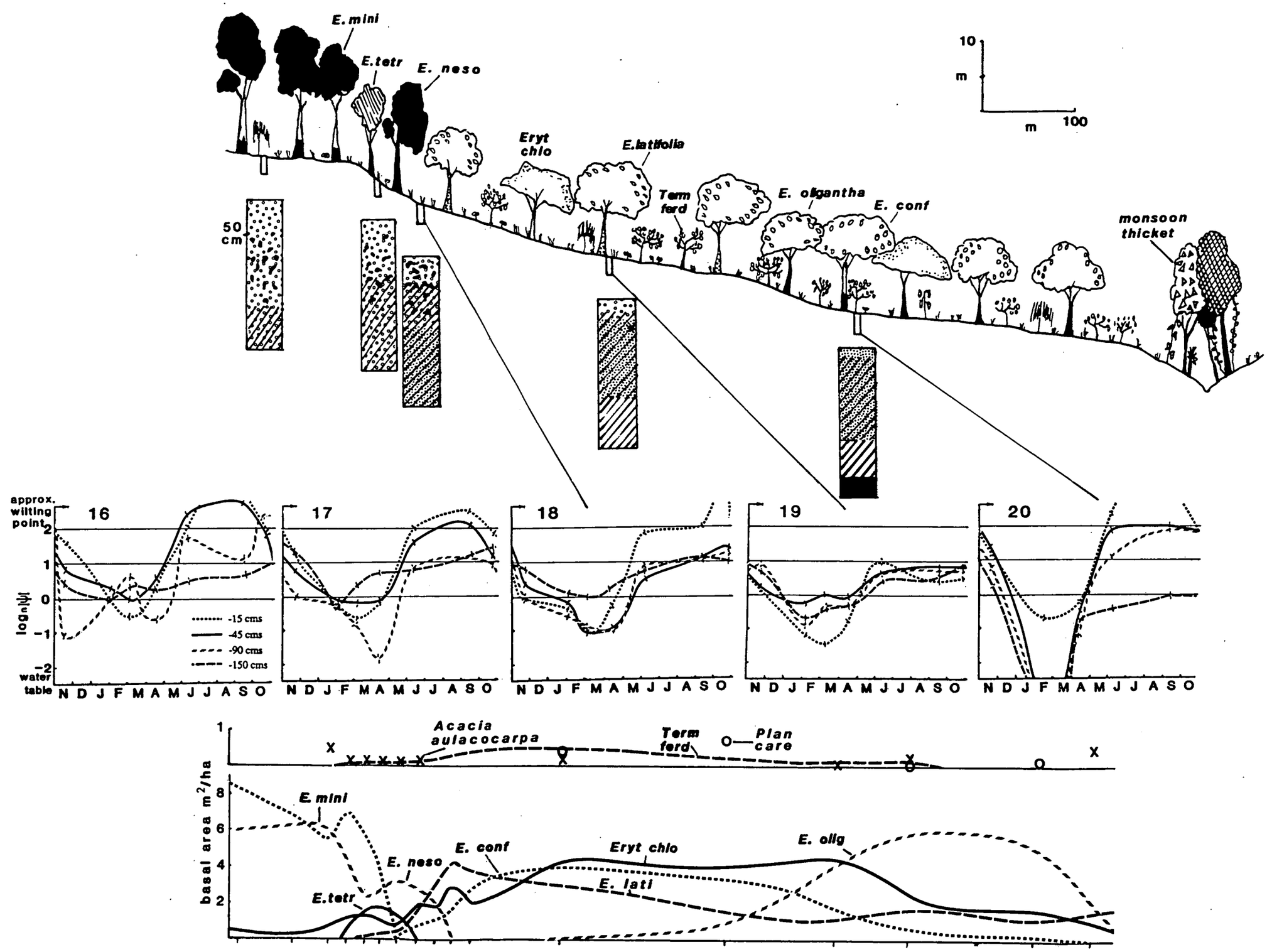


Figure 2.8 | Transect 3. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. The key to the soil profile diagrams are presented on Fig. 2.6. Approximate location of the first quadrat Melville 873 196. Approximate direction 85^0.



E. mini
E.tetr
E. neso
10
m
m
100
Eryt chlo
E.latifolia
Term ferd
E. oligantha
E. conf
monsoon thicket
50 cm
approx. wilting point
2
1
0
-1
-2
water table
log$_n$|Ψ|
16
17
18
19
20
-15 cms
-45 cms
-90 cms
-150 cms
N D J F M A M J J A S O
Acacia aulacocarpa
Term ferd
Plan care
1
basal area m^2/ha
8
6
4
2
E. mini
E. neso
E.tetr
E. conf
Eryt chlo
E. lati
E. olig

Figure 2.9 Transect 4. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. The key to the soil profile diagrams are presented on Fig. 2.6. Approximate location of the first quadrat Melville 824 048. Approximate direction 210^0.

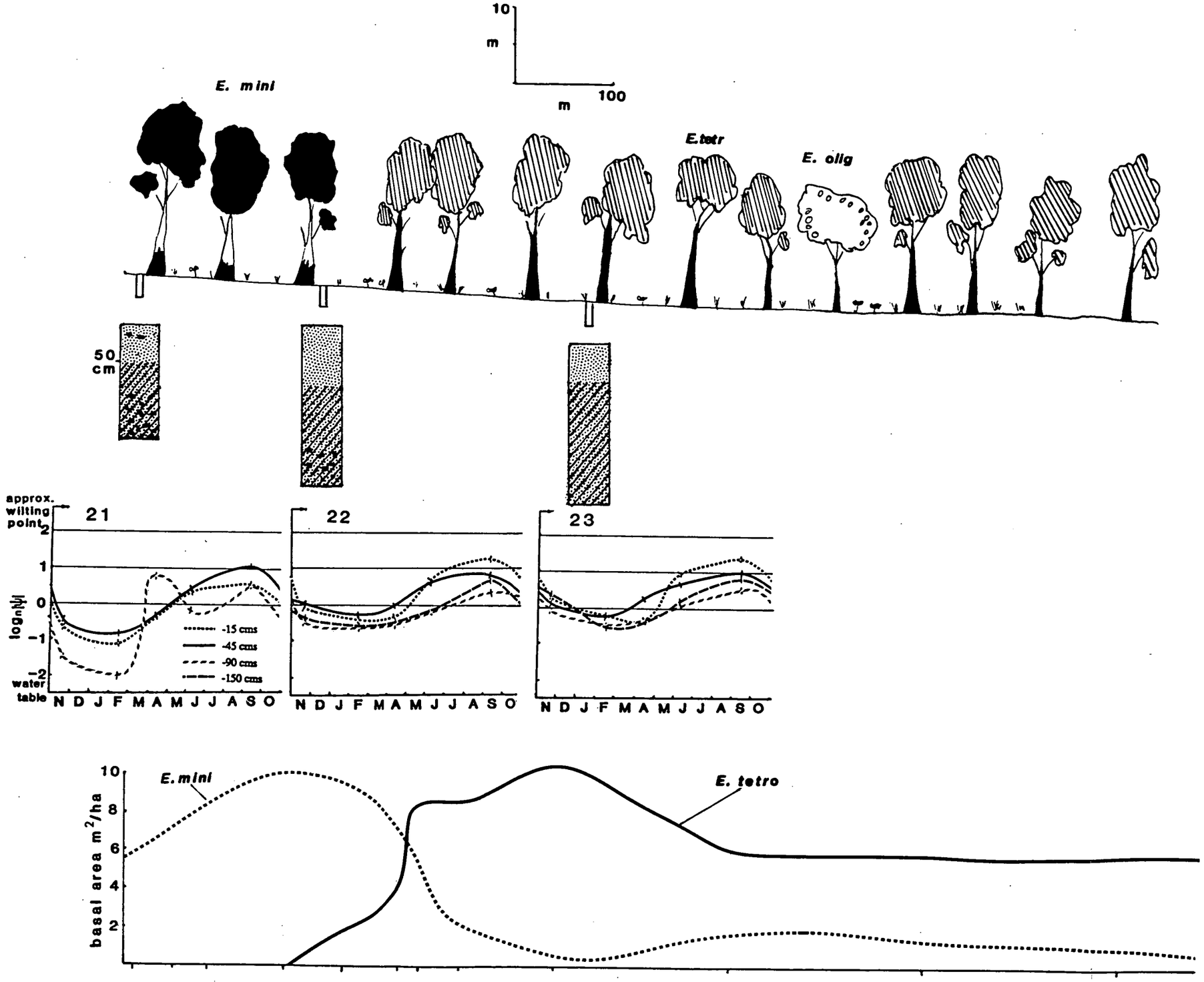


Figure 2.10 Transect 5. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. The key to the soil profile diagrams are presented on Fig. 2.6. Approximate location of the first quadrat Snake Bay 647 312. Approximate direction 310^0.

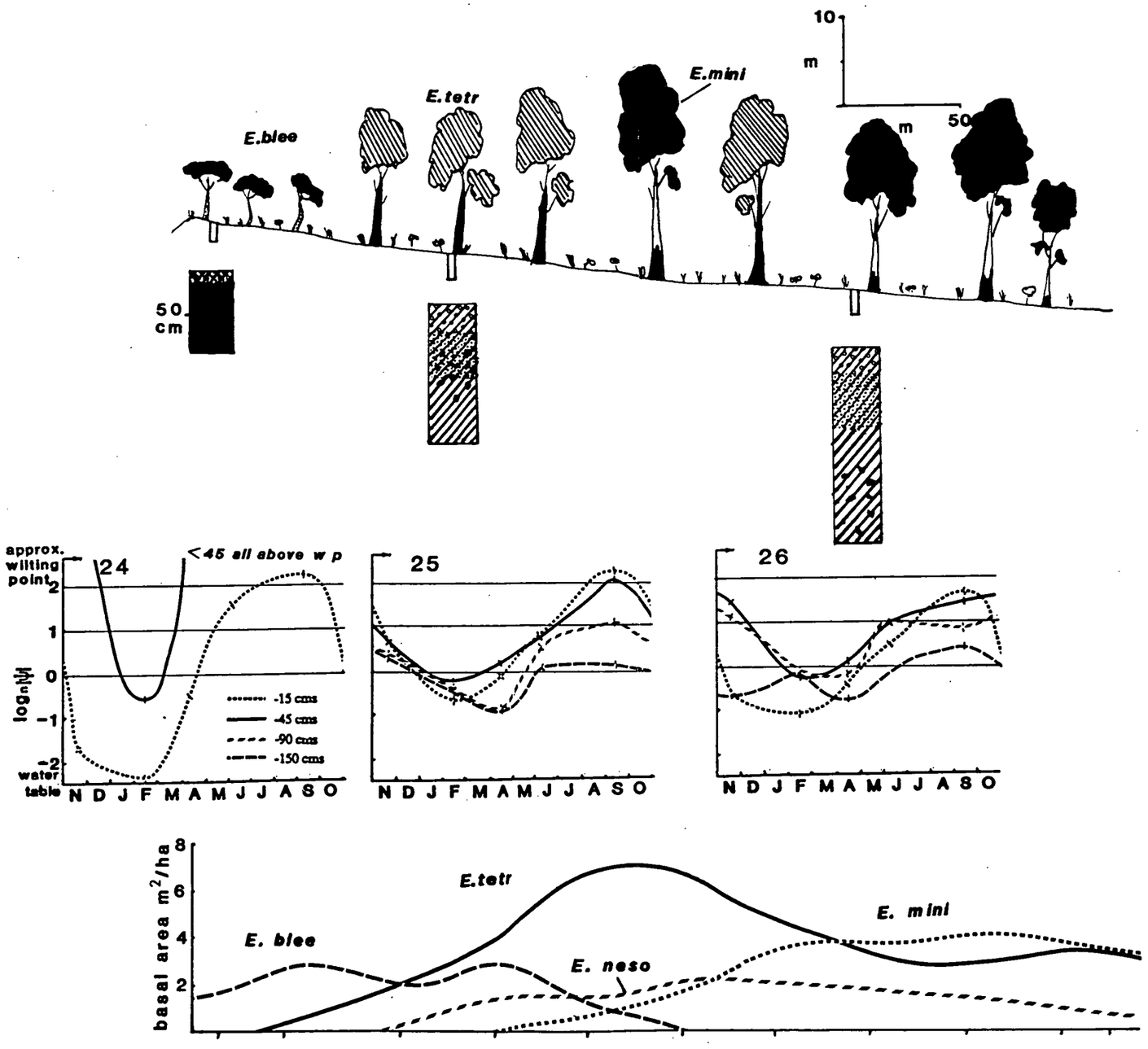


Figure 2.11 Transect 6. Tree abundances are represented as running means and the vegetation sampling points are indicated on the axis. Site numbers are represented on the top left hand corner of the matric potential (Ψ) graphs. The key to the soil profile diagrams are presented on Fig. 2.6, Approximate location of the first quadrat Melville 963 006. Approximate direction 90^0.

The anomalous moisture fluctuations in gravel free soils at 15 cm (site 13, Fig. 2.7; site 19, Fig. 2.9) may reflect the difficulty of standardising samples from shallow depths where top soils are relatively dry. The problem is less evident in deeper soils because they are buffered by the soil above. Fluctuations in Ψ at site 13 (45 cm)(Fig. 2.7), site 15 (150 cm)(Fig. 2.8) and site 26 (90 cm)(Fig. 2.11) suggest that soil moisture content may be somewhat variable across profiles. These variations may result from water extraction by plant roots.

Matric potential (Ψ) derived from the gravel free soil portion, for the soils along the transects are presented in Figs. 2.6-2.11. The environmental correlates of the TWINSPAN groups are verified across the transects. Thus, the *Melaleuca viridiflora* woodland depicted in transect 2 (Fig. 2.7) occurs on extremely harsh sites with surface water tables for five months followed by the dry season period where Ψ is beyond wilting point only in the shallow top soil or for very brief periods. *Eucalyptus bleeseri* woodland occurs on the driest substrates. The sub-soil clays are never wetter than wilting point and the shallow gravelly topsoils only have moisture available during the wet months (site 24, Fig. 2.11).

Forest occurs on sites with relatively high moisture conditions that are without extended periods of free water. None of the forest soils were beyond wilting point in June and there is moisture available below 45 cm throughout the driest months in all forest profiles. The water table under forest is nearly always deeper than 2 m although free water was found within 45 cm at site 13 (Fig. 2.7) in February. This measurement is confirmed by the observation that wet season water tables were near the surface for more than a month in an area of forest where the main road had become impassable. However, 1986/87 was a relatively wet rainy season with the heaviest January rainfall at Nguiu in 12 years (Fig. 2.5). The water table at site 13 was not observed within 2 m at several inspections during the following wet season. Presumably the relatively deep porous soil of the sites that support forest enables rapid drainage. In a normal wet season, rainless periods would allow the recession of water levels and prolonged waterlogging is not an annual phenomena.

The effects of seasonal moisture regimes on vegetation structure and overstorey composition within the forest group 010 are unclear. Similar shifts in structure, abundance and habit of single species can occur not only on a variety of substrates but also with apparently disparate Ψ cycles. Thus, *Eucalyptus miniata* can become more abundant and replace *Eucalyptus tetrodonta* as dry season soil moisture appears to increase (transect 6, Fig. 2.11), decrease (transect 4; Fig. 2.9) or when the situation is equivocal (transect 5, Fig. 2.10). *Terminalia ferdinandiana* occupies the understorey of low forest where dry season moisture appears to be more available than in an adjacent forest where this species is confined to the ground layer (transect 4, Fig. 2.9). However, this species is also abundant with other broadleaved trees in the midstorey of the seasonally extreme environments that support *Melaleuca viridiflora* woodland (transect 2, Fig. 2.7). These broadleaved species are reduced to the ground layer as conditions improve (deep water tables during the wet season and available moisture for long periods during the dry season) in the *Eucalyptus nesophila* and *Eucalyptus miniata* forest at the end of transect 2 (Fig. 2.7). Tall eucalypt forest replaces woodland as conditions improve (transect 2, Fig. 2.7; transect 6, Fig. 2.11) but is replaced by low forest dominated by *Eucalyptus latifolia* on heavier soils that appear to have favourable Ψ cycles (transect 4, Fig. 2.9).

All of the relatively abundant forest species (*Eucalyptus miniata, Eucalyptus nesophila, Eucalyptus tetrodonta, Erythrophleum chlorostachys* and *Terminalia ferdinandiana*) showed apparent indifference to drought as measured by the chi-squared analysis of drought index scores. *Eucalyptus miniata* ($P<0.001$) and *Eucalyptus tetrodonta* ($P<0.01$) are disfavoured by waterlogging. The three augered sites where *Melaleuca viridiflora* occurred were drought stricken during the dry season and waterlogged during the wet season.

Given that *Eucalyptus nesophila* is confined to the highest rainfall extremes of the Top End it might be expected to occupy sites with relatively favourable dry season moisture conditions within its range. This species dominates the well drained rocky positions in the middle of transect 2 (Fig. 2.7) where soil moisture conditions are among the most favourable of those sampled. This may reflect the moisture

concentrating effect of gravel in these soils. However, at site 12 (Fig. 2.7) on this transect *Eucalyptus nesophila* dominates a gravel free site with loamy soil that is drier than forest sites dominated by other tall eucalypts (ie. site 13, Fig. 2.7).

Interpreting the Ψ cycles of deep sandy loams is not clouded by the ambiguous effects of gravel content. These soils all have similar Ψ cycles but can be dominated by forest with or without mixed shrubby understoreys (site 3, Fig. 2.6; site 14, Fig. 2.8 respectively), by *Terminalia ferdinandiana* low woodland (site 2, Fig. 2.6) or by *Eucalyptus polycarpa* woodland (site 15, Fig. 2.8).

2.3.3 Root excavation

The root excavations suggest that the replacement of evergreen forest by low forest on transect 4 (Fig. 2.9) as moisture conditions apparently improve may be misleading. The trenches exposed obvious physical differences between the soils of the forest types along this gradient. Despite gravel in the profile, the trench at site 16 was dug in 15 minutes. The backhoe was hindered by clay at site 19 and digging the trench required more than three times the energy. While a large proportion of small and medium (<1 mm and 1-10 mm) surface roots were obviously attached to understorey plants, most of the large surface roots were undoubtedly attached to overstorey trees. Table 2.2 reveals that all classes of roots were concentrated near the surface although the decline with depth was less marked for large roots. Root systems at site 19 scarcely penetrate below 60 cm and examination of tree roots at this depth revealed that it was not simply the physical barrier of the clay soils that prevented their downward growth. The decomposition of tree roots at this depth suggests anaerobic conditions despite the fact that free water was not evident for any part of the year in this profile. This situation contrasts with site 16 where deep roots of the tall eucalypts have developed despite having to weave and squeeze their way through the moderately heavy gravel layer in the middle of this profile.

Table 2.2 Frequency of roots per 0.1 m^2 on a vertical soil surface.

Depth	Root diameter <1 mm	1- 10 mm	>10 mm
Forest			
0-20 cm	33.80	10.00	1.89
20-40 cm	10.67	3.89	1.00
40-60 cm	4.00	1.33	0.44
60-100 cm	1.11	1.11	0.28
100-140 cm	0.22	0.39	0.11
Low forest			
0-20 cm	36.67	7.33	1.67
20-40 cm	9.11	3.88	0.55
40-60 cm	2.44	1.67	0.11
60-100 cm	0.39	0.33	0.00
100-140 cm	0.00	0.06	0.00

2.4 Discussion

This study and concurrent work on Melville Island (Wilson 1991) present the first data on seasonal moisture cycles in the savanna vegetation of Australia's monsoon tropics. No data are available from Africa although similar work from savannas in South America has been synthesised by Sarmiento (1984). In terms of physiognomy and seasonal soil moisture conditions it seems that South America has no analogue to the forests of Melville Island. Most South American savanna types suffer the severities of soil waterlogging and drought and the different types can be distinguished by variations in the degree of these effects. Evergreen eucalypt forests on Melville Island are not subject to extreme moisture conditions as determined by Sarmiento (1984); the depth of the water table in the wet season or the length of the period where Ψ is below -15 bars (approximately wilting point). One of the savanna types reported from Guyana (Eden 1964) has moisture cycles comparable to the driest Melville Island forest (site 16). This vegetation type is described by Sarmiento (1984) as semi-seasonal savanna and is the only open vegetation in monsoonal South America with a tree layer. Savanna with forest structure is exceptional

in the Llanos of northern South America (Blydenstein 1967, Sarmiento 1983) and the Cerrado of Brazil (Cole 1960, Eiten 1975) despite most of their area having climatic regimes that are similar to the monsoonal tropics of Australia (Strahler 1975). This suggests that the moisture holding capacities of the soils may be different between these Australia and South America or that there are few species in South America that match the success of eucalypts in the tropical monsoon environment. Clearly more soil moisture data from across tropical Australia and throughout the monsoonal regions of other continents is required.

The environmental determinants separating community floristics in the savannas of Melville Island were elucidated in this study, as has been achieved from other phytosociological studies of northern Australia (eg. Langkamp *et al.* 1981, Bowman and Minchin 1987, Kirkpatrick *et al.* 1987). However, it proved more difficult to establish the environmental correlates of floristic patterns within vegetation communities. Most quadrats were from the evergreen savanna forest dominated by mixtures of *Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta* and the cause of floristic pattern within this forest type was not determined during this study. However, it is clear that the patterns of structure and overstorey composition within savanna forests are not always parallel. This has been observed for other savanna environments in the Top End (Rice and Westoby 1985).

A major part of this chapter has sought to understand the importance of subsurface soil moisture conditions as a determinant of overstorey compositon and structure. However, an understanding soil moisture relations is confounded by the influence of gravel (Reinhart 1961) and there are no reports in the literature that quantify this relationship under natural conditions. Magier and Ravina (1984) provide evidence from irrigated orchards that the growth of pears (*Pyrus malus*) is enhanced by coarse gravel content up to 30% volume. They also report the work of Magduf and Garti (1971), who found that fine dense gravels inhibited the growth of apples (*Malus sylvestris*). In some situations, gravels and rocks may also increase the aeration of soils (Magier and Ravina 1984). Thus, gravels and rocks can have positive and negative effects on soil moisture conditions and the relative strength of these influences is determined by overall moisture

regimes, gravel density, the nature of the soil matrix and possibly the shape of the inclusions (Dunn and Mehuys 1984).

Some authors have noted that surface gravel correlates with vegetation patterns in northern Australia (Bowman 1986, Bowman and Dunlop 1986, Kirkpatrick *et al.* 1987, Bowman *et al.* 1988c). While Edwards *et al.* (1984) suggest that moisture decreases for the total soil volume as rockiness increases, this study has demonstrated that rockiness concentrates moisture in the gravel free spaces and that the conditions in this space are wetter than they would be without rock. However, at the scale of this study there is no clear relationship between vegetation and moisture that has been concentrated in the gravel free portion of the soil. While conditions in the soil space may be favourable, the ability of plant roots to access this moisture may be hindered by dense gravel layers, rockiness or high density soils. The presence of tap roots under forest trees at site 16 (Fig. 2.9) and where they are exposed in eroding sea cliffs on Melville Island (Plate 2.1), and their absence under the deciduous eucalypts at site 19 (Fig. 2.9) suggests that forest trees have a requirement for substrates that allow the development of a deep tap root. However, underground barriers do not in themselves prevent the development of forest. At Werner's (1986) study site excavations revealed that almost all *Eucalyptus tetrodonta* and *Eucalyptus miniata* forest trees had root systems confined to soil above a rock barrier at about 55 cm. This is verified by the observation of forest perched on shallow soils mantling rock on Melville Island where this situation has been exposed by road cutting (Fensham pers. observ.). Forest is supported on extremely rocky ground at site 7 on transect 2 (Fig. 2.7). In a comparable topographic position heavy soils inhibit forest development at site 8 (Fig. 2.7). It seems that the forest species are prevented from establishing on clay sites by poorly aerated conditions. The low porosity of clay may mean poor aeration despite deep water tables. This suggestion is validated here by the presence of decomposing roots in clay soils without extended periods of waterlogging. Porosity can be approximated from bulk density and the measurement of this variable should be critical to further studies. An examination of some data for tropical soils reveals that field texture is a poor surrogate for bulk density (Prebble 1970, Calder and Day 1982).

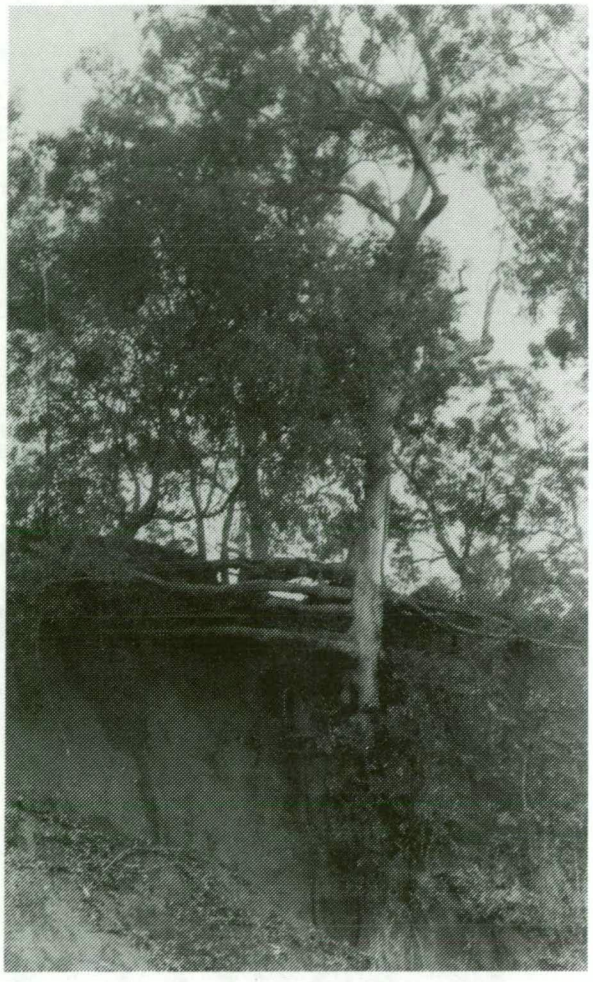


Plate 2.1 Root system of *Eucalyptus tetrodonta* exposed on sea cliffs

Bowman (1988) proposed that broadleaved species enter the midstorey of forest in situations where dry season moisture conditions are sufficiently favourable for growth to exceed the damaging effects of fire. This hypothesis seems incorrect for the transects presented in this study. Vegetation types with broadleaved midstoreys occur on clay (site 5, 6, 8, 11, 18 and 19) and the deep sandy profiles of site 3 where moisture conditions are virtually the equivalent of those under the more open forest of site 1.

The Ψ cycle of the semi-deciduous low forest (site 19; Fig. 2.9) appear to be more favourable than the evergreen forest on the same transect (site 16; Fig. 2.9). However, the dominance of the deciduous lifeform and the slower growth rates of woody sprouts on this site (Chapter 3) suggests that this is probably not the case. Tree roots were more prevalent at depth in the sandy soils of the forest compared to the heavier soils under the low forest (Table 2.2). Furthermore, the deep sandy profiles all have more moisture available at 45 than 90 cm despite evaporative effects being greater at shallow levels. There is a correlation between increasing depth and Ψ for the soils without deep sandy profiles ($P<0.001$). The lower than expected moisture contents around 90 cm in light soils may result from the absorptive demand of tree roots in this zone.

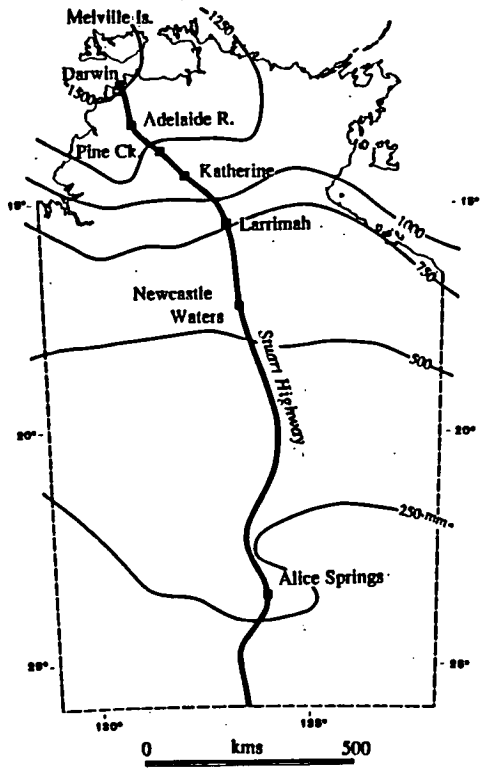
The possibility that waterlogging during extreme wet years determines vegetation patterns seems remote. The 1986/87 wet season was relatively wet and water tables were near the surface in forests that are normally well drained. Site 2 (Fig. 2.6) had no tall trees and no evidence of free water despite this site having a poorly permeable basement of kaolinitic substrate at 210 cm and a topographic position that could conceivably provide the metre or so of water required to swamp such a profile.

Southern distribution limits and tolerance to soils with moisture regimes beyond wilting point in the dry season are two possible surrogates for drought tolerance. The distributions of eight common Top End tree species used throughout the experimental sections of this thesis and *Eucalyptus nesophila*, a common dominant of Melville

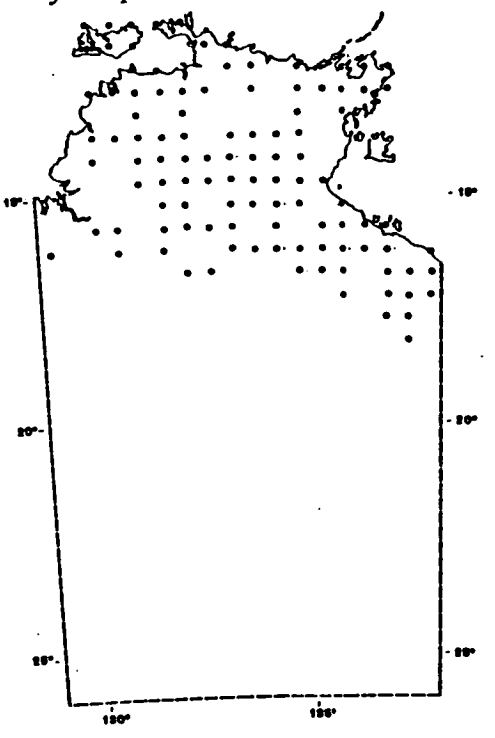
Island forest are presented in Fig. 2.12. *Erythrophleum chlorostachys* and *Eucalyptus confertiflora* extend furthest inland and are present at south of Newcastle Waters on the edge of the desert region. The occurrence of these species in relatively low rainfall zones is not mirrored by the distribution of these species across local moisture gradients. This fact suggests clinal variation in the ecological tolerance of these species.

Difficulties in separating the moisture tolerance of the Top End's most common tree species, *Eucalyptus miniata* and *Eucalyptus tetrodonta,* across local gradients on Melville Island are reflected by similarities in their range extensions. The distributions of *Buchanania obovata, Eucalyptus miniata, Eucalyptus tetrodonta* and *Planchonia careya* are very similar and all of these species occur throughout the monsoonal region of the Top End. None of these species occur where mean annual rainfall is less than about 600 mm. *Acacia aulacocarpa* and *Terminalia ferdinandiana* have more limited distributions than *Buchanania obovata, Eucalyptus miniata, Eucalyptus tetrodonta* and *Planchonia careya,* although there lower rainfall limits are similar. *Terminalia ferdinandiana* extends into the central inland region of the Top End and *Acacia aualacocarpa* has a more coastal and sub-coastal distribution. *Eucalyptus nesophila* is known from the highest rainfall environments of the Top End where it is known from the Tiwi Islands and Coburg Peninsula. However, this eucalypt can dominate forests on deep sandy soils (eg. Fig. 2.8) or where soils are relatively shallow and heavy with dense gravel beds (Fig. 2.7) where access to deep soil moisture reserves is likely to be limited.

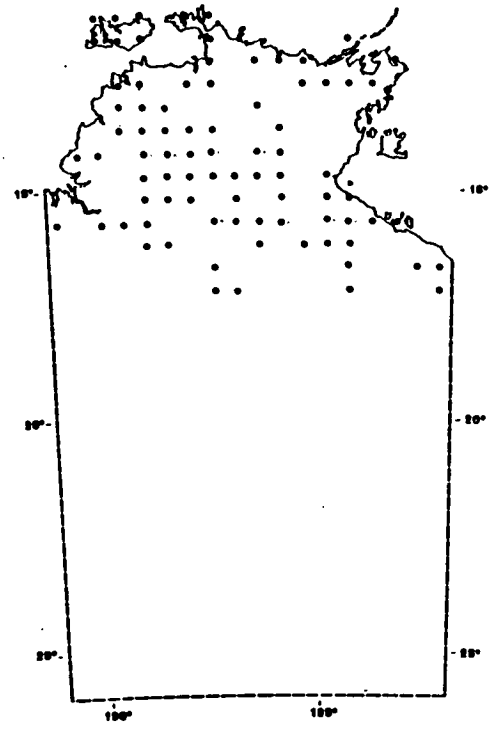
Understanding the moisture relations of our tropical soils and how physical attributes such as soil density and rockiness affect Ψ cycles and root growth will require further research. Any attempts at the approach explored here should concentrate on rock free soils until the interplay of the physical attributes of soils and their effects on moisture availability are better understood. This study has also raised the possibility that other hypotheses involving nutrients and their interactions with moisture and fire regimes should be given further consideration. In this study magnesium and calcium correlated



Erythrophleum chlorostachys



Eucalyptus confertiflora



Eucalyptus tetrodonta

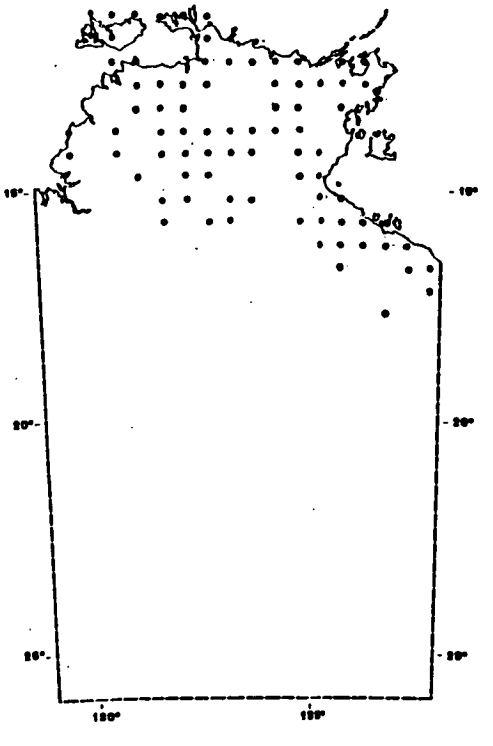
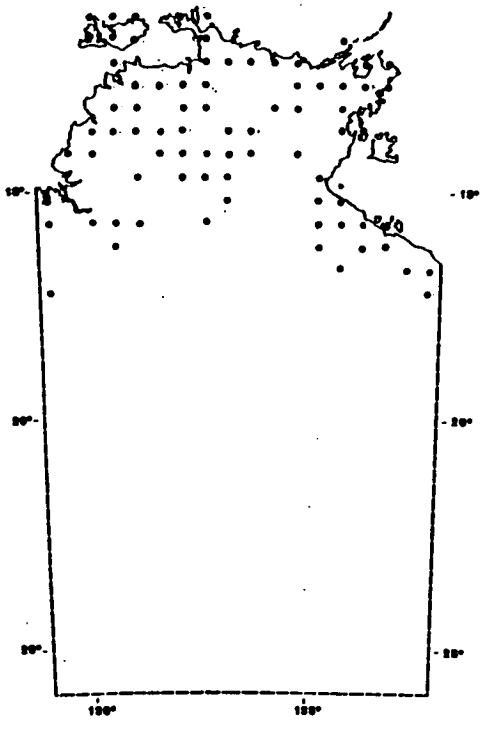
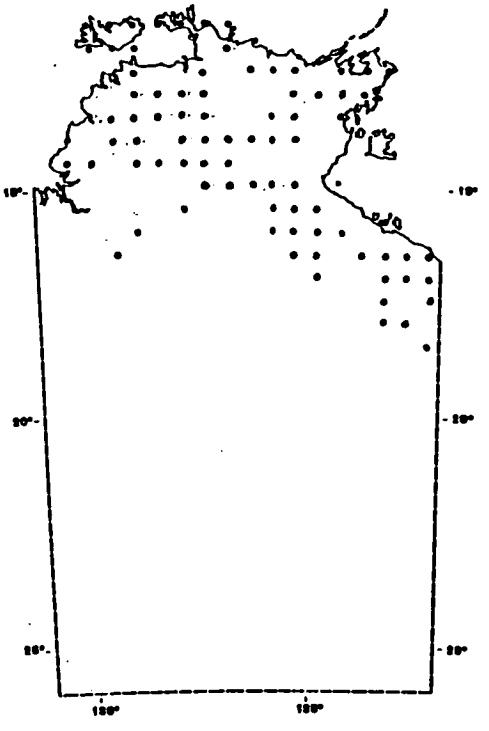


Figure 2.12 Northern Territory locality map and the distributions of nine open forest tree species. Information on species limits was obtained from collections held in the Darwin Herbarium, from the data base of the Northern Territory vegetation map (Wilson *et al.* 1990) and tree species lists from 45 plots along the Stuart Highway from Newcastle Waters to Darwin (Fensham unpublished).

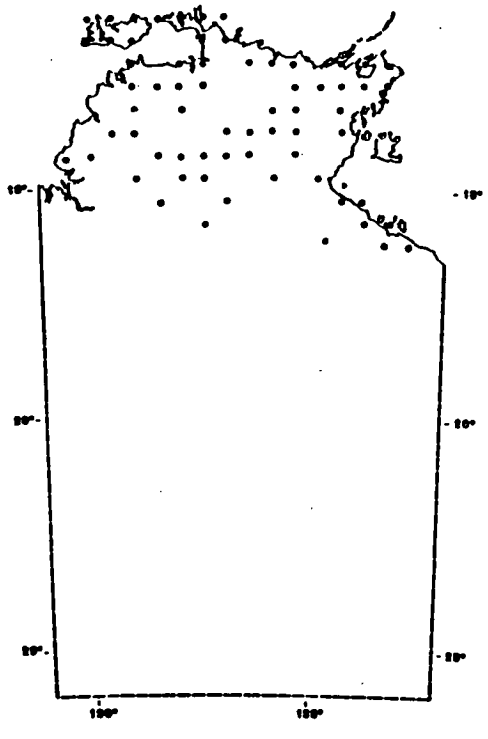
Buchanania obovata



Eucalyptus miniata



Planchonia careya



Terminalia ferdinandiana

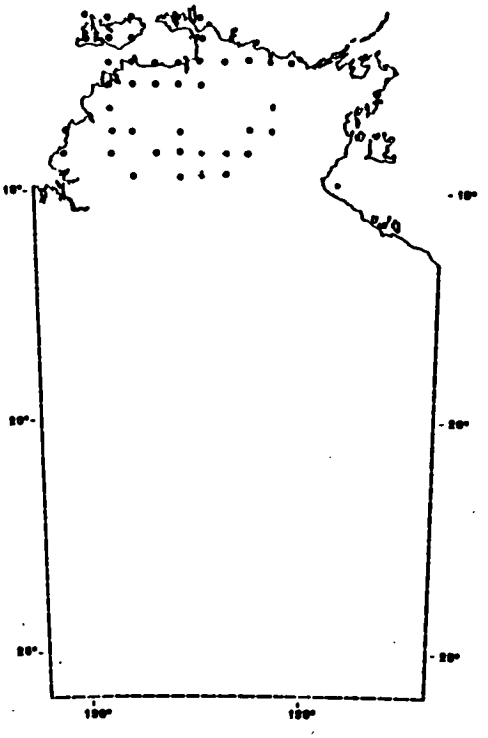
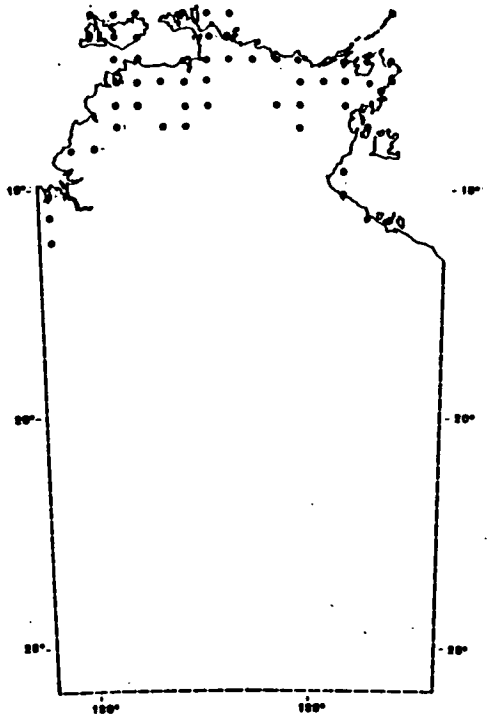


Figure 2.12 continued

Acacia aulacocarpa



Eucalyptus nesophila

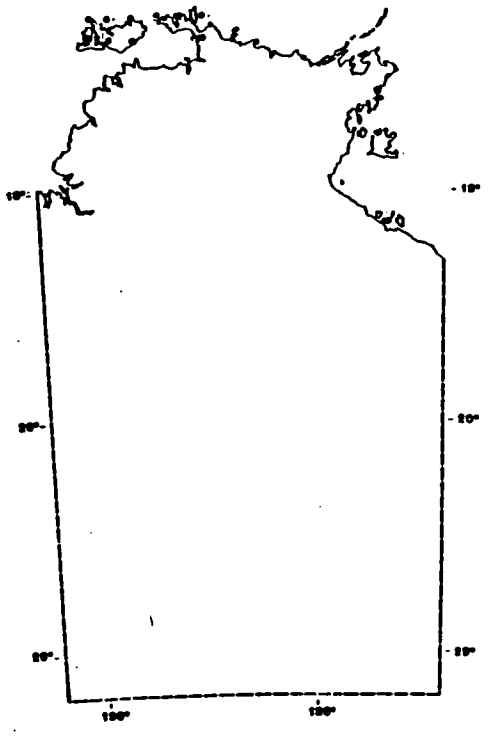


Figure 2.12 continued

strongly with floristic gradients. These elements are not important environmental correlates in the savanna vegetation of Brazil (Lopes and Cox 1977) or on Groote Eylandt in the Northern Territory (Langkamp *et al.* 1981). However, the suggestion that they may be important influences affecting some patterns in tropical Australia should be considered because similar correlations have been presented by Wilson (1991) from Melville Island and Isbell and Smith (1976) from Cape York.

Concomitant shifts in species dominance, vegetation structure and soils testify to the importance of edaphic gradients for determining some overstorey patterns. This is true for environmental gradients that are steep enough to effect concurrent shifts in overstorey and understorey. This is the case with *Melaleuca viridiflora* and *Eucalyptus bleeseri* woodland. In these situations the nature of the relationship between soil and vegetation can be described in terms of soil moisture regimes. In other situations vegetation gradients are associated with soil catenas and almost certainly relate to edaphic conditions although the precise nature of the relationship could not be elucidated. This is the case with the separation between the deciduous low forest and the evergreen forest on transect 4 (Fig. 9). The relatively heavy soils under the low forest inhibit root development despite soil moisture conditions being favourable. There are other situations where the composition or structure of the overstorey changes without obvious shifts in edaphic conditions (ie. transect 3; Fig. 2.8). The open vegetation at the beginning of transect 2 (Fig. 2.7), the occurrence of *Eucalyptus tetrodonta* at site 17 (Fig. 2.9) and *Terminalia ferdinandiana* at site 2 (Fig. 2.6) are not clearly related to edaphic conditions. These vegetation formations are distinctive and homogeneous but cover only small areas (ie. <0.5 ha). Patch dynamics may play a role in determining some of these patterns. The production of fruit in *Eucalyptus miniata* and *Eucalyptus tetrodonta* is limited (Section 8.2) and some species may have specific germination and early growth requirements. The availability of seed, the weather conditions of the following seasons, the fire regimes of those seasons, micro-environmental conditions and the competitive effects of the surrounding vegetation may all combine to determine the composition of a regenerating patch. The coincidence of random

historical events and the phenology and life-stage of the tree species at a site may determine some of the structural and compositional patterns at the mesoscale in the tropical savanna forest. These dynamics are the subject of subsequent chapters of this thesis.

CHAPTER 3 PATTERNS AND DETERMINANTS OF WOODY GROWTH IN THE TROPICAL EUCALYPT FOREST

3.1 Introduction

Correlative studies have made a substantial contribution to an understanding of the environmental controls of vegetation pattern in northern Australia (see Bowman's 1988 review). Studies such as these pervade the ecological literature and are founded on the understanding that vegetation change across gradients is a function of the overlapping response of species to the conditions that influence their establishment, growth, reproduction and survival.

The interplay of growth rate and environment has been invoked as a determinant of vegetation structure in tropical eucalypt forest (Braithwaite and Estbergs 1985, Bowman 1988). These authors suggest that the frequent fires that burn the tropical eucalypt forest may limit structural development in some edaphic situations. While the importance of site/fire/growth interaction has been intimated, the relationship between growth and environment has never been documented for monsoonal Australia.

Dunlop (1988) has observed that the growth of woody species in the ground layer of open forest occurs well before the arrival of wet season rain. The phenomenon whereby growth occurs out of kilter with available moisture has been recorded in other tropical regions with seasonal climates (eg. Hopkins 1970a, b, Daubenmire 1972, Monasterio and Sarmiento 1976, Alvim and Alvim 1978). This perplexing situation is further complicated in the eucalypt forest of monsoonal Australia because the ground layer is burnt annually. Growth in this stratum may simply represent refoliation following fire. Clearly there is a requirement to examine growth in relation to seasonal climatic variation and environmental gradients. It specifically addresses the hypothesis that the relative success of trees (as indicated by their prevalence as upper canopy dominants) in a particular edaphic environment will be reflected by the relative growth rates of the woody sprouts of these species. This hypothesis is tested along a vegetation graident from evergreen forest to deciduous low forest. The xylem

pressure potential of woody sprouts along this gradient were measured in order to determine the relative moisture stress of trees along this gradient.

Studies on tree growth in relation to seasonal cycles may provide information on resource limitations. For example, if growth is occuring in the driest seasons this suggests that moisture is not limiting. The growth of woody sprouts in relation to seasonal cycles of soil moisture availability was determined and this study also includes the documentation of cambial growth in mature trees through the year.

The lateritic soils of northern Australia are intrinsically infertile and their depauperate status may inhibit structural development in the tropical eucalypt forest. This study includes a fertilization experiment designed to address the hypothesis that woody sprout growth is limited by nutrient availabiltiy.

3.2 Methods

3.2.1 Woody sprout growth

Transect 4 (Fig. 2.10) was chosen for the study of lignotuberous stem regrowth. This gradient traverses a forest dominated by 25 m high (H) *Eucalyptus miniata,* a small patch of *Eucalyptus tetrodonta* (20 m H) forest and *Eucalyptus latifolia/Eucalyptus confertiflora* low forest (15 m H). The forest canopy dominants are absent from the low forest. *Acacia aulacocarpa* is an infrequent tree in both vegetation types. *Eucalyptus confertiflora* and *Erythrophleum chlorostachys* commonly reach the upper and *Terminalia ferdinandiana* the mid-canopy in the low forest but these three species rarely leave the ground layer in the forest. *Planchonia careya* is occasionally a tree in the low forest but rarely occurs above ground level in the forest. *Buchanania obovata* rarely leaves the ground layer in either community. All of these tree species, with the exception of *Eucalyptus tetrodonta* and *Eucalyptus miniata* in the forest and *Eucalyptus latifolia* in the low forest are frequent as lignotuberous resprouts in all forest types.

The entire transect was burnt in mid-July 1986. Woody sprouts of the following species were monitored in:
a) the *Eucalyptus miniata* forest (A1); *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus confertiflora, Eucalyptus miniata, Eucalyptus tetrodonta, Acacia aulacocarpa.*
b) the *Eucalyptus tetrodonta* forest, at the limit of *Eucalyptus miniata*'s occurrence (A2); *Eucalyptus miniata, Eucalyptus tetrodonta.*
c) the ecotone between the *Eucalyptus tetrodonta* forest and the *Eucalyptus latifolia/Eucalyptus confertiflora* low forest, at the limit of the occurrence of *Eucalyptus tetrodonta* (A3); *Eucalyptus tetrodonta.*
d) the *Eucalyptus latifolia/Eucalyptus confertiflora* low forest (A4); *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus confertiflora* and *Acacia aulacocarpa.*

These sites coincide with sites 16-19 on Fig. 2.10. The minimum area that encompassed at least 22 individuals of each of the above target species was defined at each site by tagging trees. Sample sizes were relatively high becasue the physiological condition of the root systems and regenerating organs to which the woody sprouts are attached may be variable. A1 was 0.23 ha, A2 0.03 ha., A3 0.02 ha and A4 0.08 ha. All individuals of species with low densities were tagged. Twenty-five individuals of frequent species were randomly located in the following way. The first five or six individuals located by spirally searching from five points well spaced within the plot were tagged. At each site the individuals were mapped and tagged using indentable brass tags and pipe cleaners. Each stem of each individual was measured on ten occasions between October 1986 and June 1988. The plots were fire protected by burning around their perimeters early in the dry season of 1987. The fire escaped into portions of A1 and A2 and burnt some individuals, including most of the *Eucalyptus tetrodonta* at A1.

Plants that had broken away from the ground layer to become saplings (defined here as > 150 cm H or >2 cm diameter at the base) at any individual sampling time were tagged and measured. The eight tallest *Acacia aulacocarpa* individuals from the 38 that satisfied the sapling criteria on the 11/11/87 were tagged.

Seasonal soil matric potential information was gathered in the manner described in Section 2.2.

3.2.2 Xylem pressure potential

Measurements of xylem sap pressure potential were made using a pressure bomb (Scholander *et al.* 1965) in the middle of the dry season (4/9/87). Measurements were performed on tree and lignotuberous lifeforms of several species between the sites on Transect 4 (Fig. 2.10). Measurements for all species were taken between 8 and 10 am.

3.2.3 Response to fertilizer

Twenty-two individuals of the eight monitored forest species were tagged in a plot surrounding A1 and were measured in mid-March 1987. At this time 130 g of fertilizer (11% nitrogen, 7% phosphorus, 8% potassium) was spread around the base of each individual within a circle of 1 m radius. The fertilizer was scratched into the surface soil with a rake. These individuals were measured subsequently at the end of the following dry season (8-10/11/87) and at the end of the following wet season (20-22/4/88). The escaped fire of the 1987 dry season burnt about half of the fertilized individuals and these were considered as a separate fertilized and burnt treatment. The unburnt, unfertilized plants in A1 (Section 3.2.1) provided a control.

3.2.4 Clipping versus burning

Two plots were established in a forest nearby and similar to A1. Tagged wire hoops were placed over ten lignotuberous individuals of the eight forest species. The stems of all plants were measured. The following treatments were performed in mid-June 1987. In the first plot all stems of each individual were clipped to ground level. The second plot was burnt so that all the aerial biomass of the lignotuberous plants was destroyed. All stems of each individual were measured soon after emergence (10-12/8/87) at the end of the dry season (19-21/11/87) and after the following wet season (14-16/4/88).

3.2.5 Mature tree growth

Seasonal growth of mature individuals was determined from a forest dominated by *Eucalyptus miniata* (site 3, Fig. 2.7) which included individuals of the eight monitored forest species as mid and upper canopy members. Seasonal soil moisture cycles are available for this site (Section 2.33). A nail and tag was hammered into ten individuals of each species at breast height or below the lowest branch. Large trees are difficult to measure accurately and only individuals less than 1000 mm circumference were selected. The girth of each individual was measured to the nearest millimeter immediately above the point of nail insertion. Each measurement was performed at least twice each sampling time, and the lowest value accepted. Seven measurements were taken between 10/8/87 and 23/11/88.

3.2.6 Analytical methods

Analysis of lignotuberous growth was performed on the height of the tallest stem unless otherwise stated.

The mean and individual growth data from the measured plots was prepared graphically for each species. A simple classification of growth patterns was prepared and the chi-squared test was used to examine the preference of species for particular patterns. Growth of each individual was calculated as:

$$\frac{H_2-H_1}{t_2-t_1}$$

where: H_2 and H_1=heights at consecutive measurements; t=time.
Matric potential at 45 cm depth at the mid-time of each sampling period was extrapolated from Fig. 3.1. Matric potential was correlated with mean growth using Pearson's product moment correlation coefficient.

Further analysis was performed following the computation of a relative growth measure (R) where:

$$R=100 \times (\log_n H_1 - \log_n H_0)$$

where: H_0 = plant height at 128 days; H_1 = plant height at final measurement.

This equation allows for variations in initial plant size (Radford 1967), and a $\log_n(x+1)$ transformation was employed to improve the normality of R. The difference in R between species and site was explored using two-way ANOVA. R values that were significantly affected by species or site as a main effect were subjected to the Student-Newman-Keuls multiple range test to determine which pairs of species and sites were significantly different. Individuals burnt in the escaped fire were excluded from analysis unless indicated.

For the fertilization and clipping experiment, the height and numbers of stems were divided by their original values prior to analysis. Differences between treatments for these characters were compared using the Mann-Whitney U-test.

Comparison of potential differences in xylem pressure between sites was attempted by dividing the measurement for each individual by the mean xylem pressure potential for that species-lifeform group. This reduces sampling bias resulting from large differences between species and lifeform. These standardized values were compared between the low forest (A4) and the forest (A1) using the Mann-Whitney U-test. The same test was used to explore differences between individual lifeforms, species and sites.

Growth rates of mature trees were calculated by determining the mean of the increment difference from the starting circumference of all individuals of each species.

3.3 Results

3.3.1 Generalized patterns of woody sprout growth

Fig. 3.1 traces the mean growth rates of tree species for two years after a fire in July 1986. With the exception of *Acacia aulacocarpa, Eucalyptus tetrodonta* and *Erythrophleum chlorostachys* at A1, the general growth trend is mirrored for each species at each site. *Eucalyptus tetrodonta* at A1 has an exceptional growth pattern but this is probably an artefact of the small sample that consists of only three individuals that survived the accidental burning of part of this plot during the 1987 dry season. All species at all sites show the most rapid growth in the first 3 months after fire although *Planchonia careya* and *Terminalia ferdinandiana* were slower to emerge than other species. Following the initial period of rapid growth, the mean height of most species either sharply declined or ceased for the remainder of the sampling period. *Acacia aulacocarpa* and *Erythrophleum chlorostachys* at A1 show slight increases in height after the initial burst in the first post-emergence months. The onset of growth dormancy is coincident with the arrival of wet season rain and increases in available soil moisture (Fig. 3.1). Mean height does not increase in the following dry season and for many species declines due to the death of above-ground parts. It is not until the following wet season that the mean height of most species shows a slight increase. Thus, growth occurs during the dry season following removal of above-ground biomass by fire and does not occur again until the wet season of the following year. Because of this growth pattern there is no correlation between seasonal growth and soil moisture for any species at any site ($P > 0.05$ in all cases).

Almost all woody sprouts, with the exception of *Acacia aulacocarpa* at A1 remained less than 1 m H in the ground layer following 2 years of fire protection. It is difficult to evaluate the growth characteristics of individuals that breakaway from the ground layer because of the low density of saplings. However, the tallest non-acacia breakaway sapling in the 0.36 ha of total plot area was a *Eucalyptus miniata* that attained 2.7 m H (Fig. 3.2). No saplings were sufficiently large enough to survive the 1988 dry season fire. The tallest *Acacia aulacocarpa* sapling

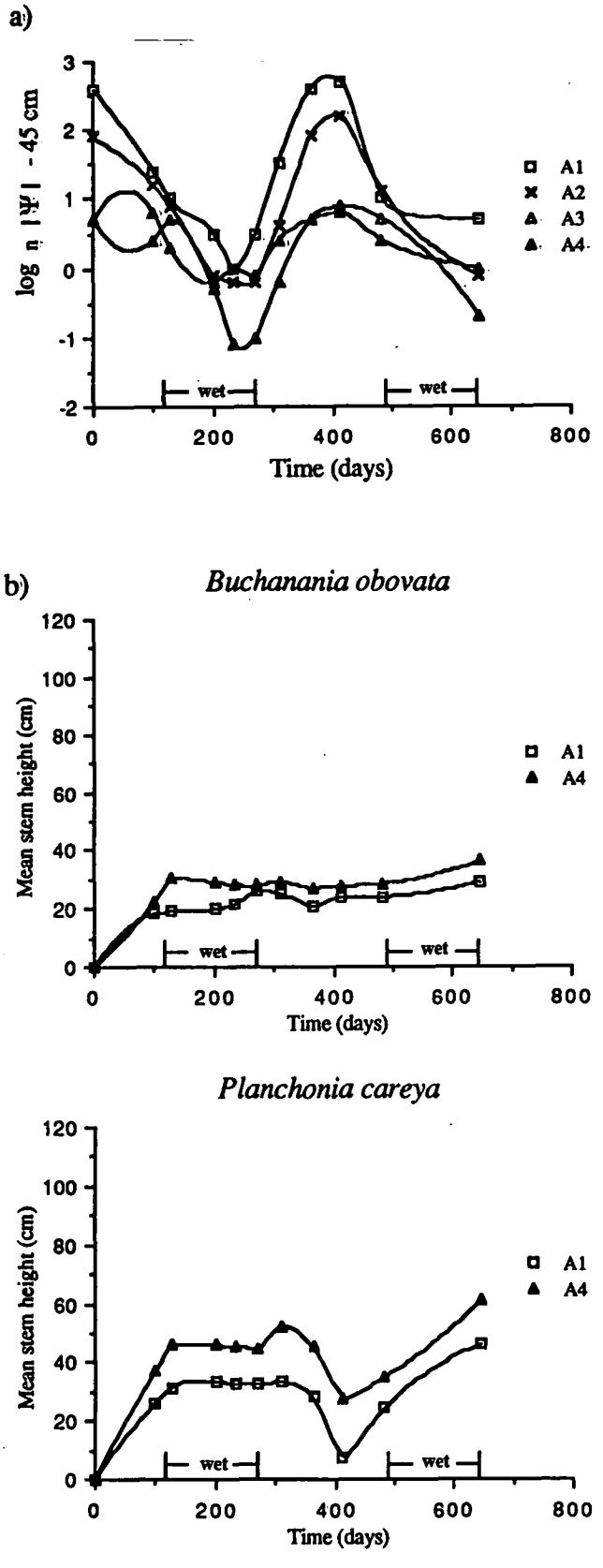


Figure 3.1 a) Seasonal matric potential (Ψ) cycles at 45 cm of the four study sites; b) Mean height of the tallest stem of woody sprout regrowth of eight tree species at the study sites. The wet season periods are marked on each graph.

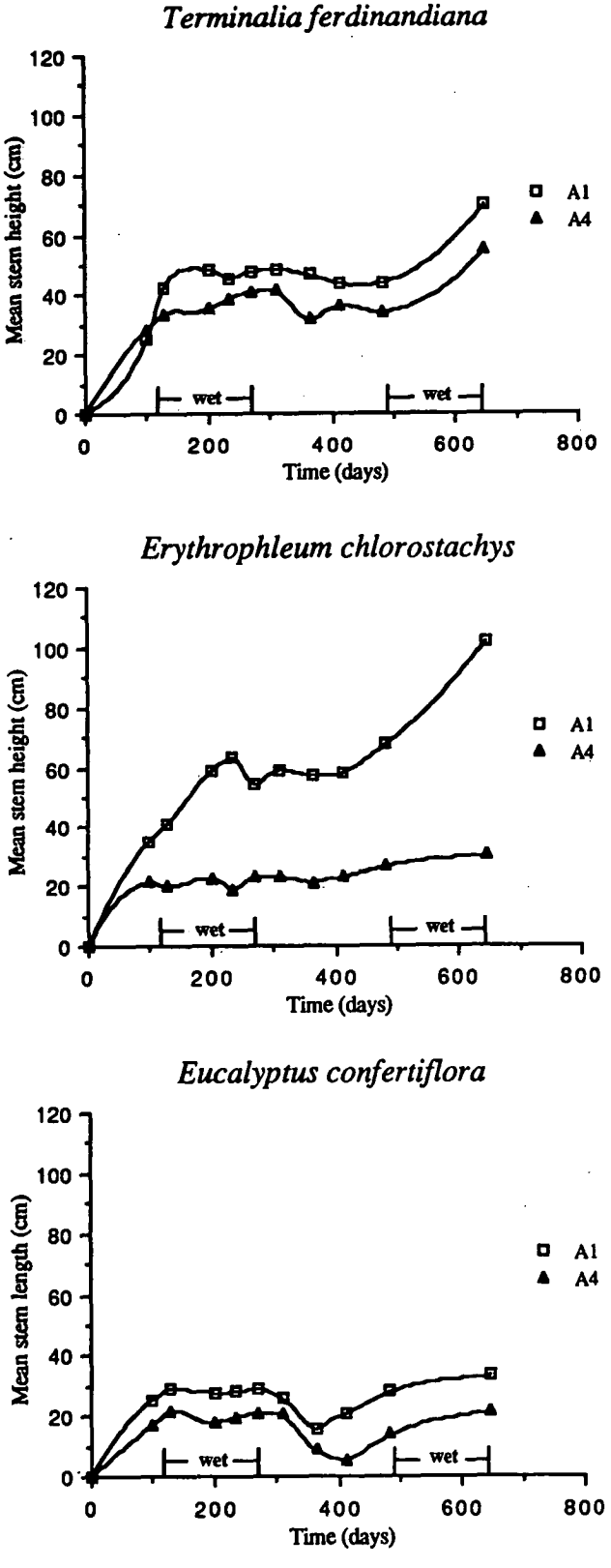


Figure 3.1 b) continued

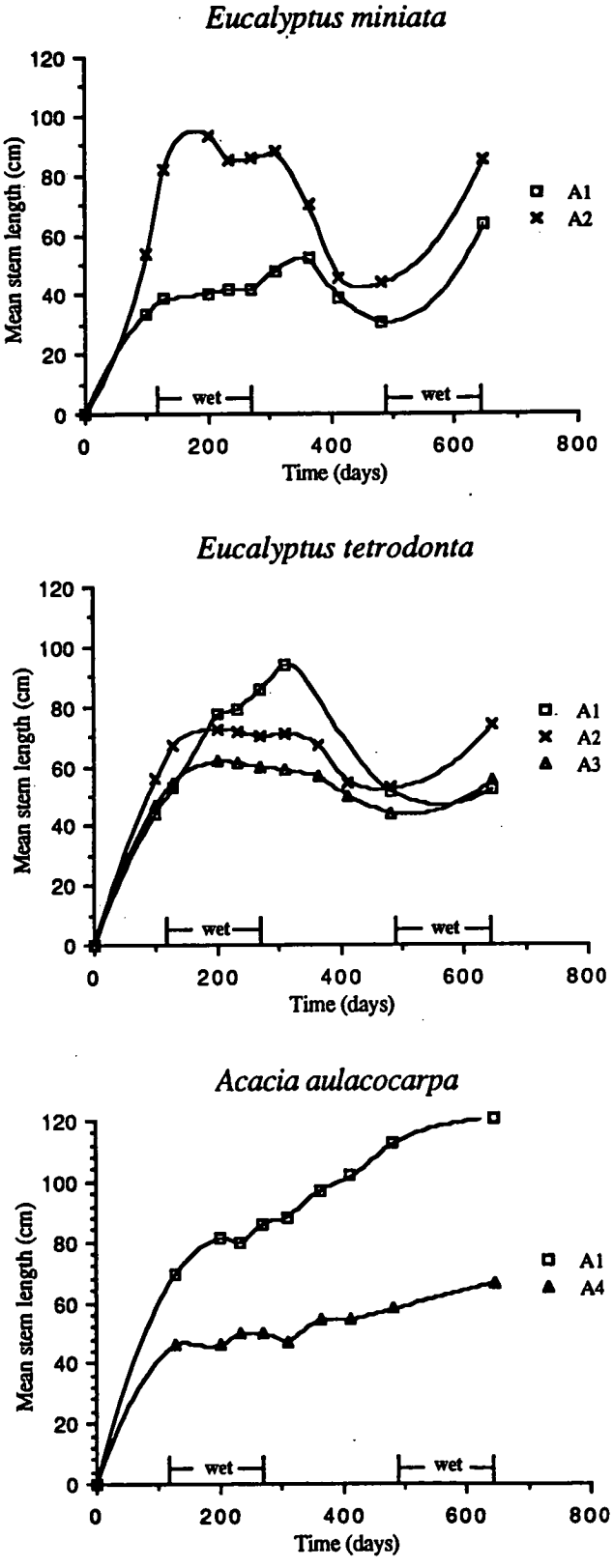


Figure 3.1 b) continued

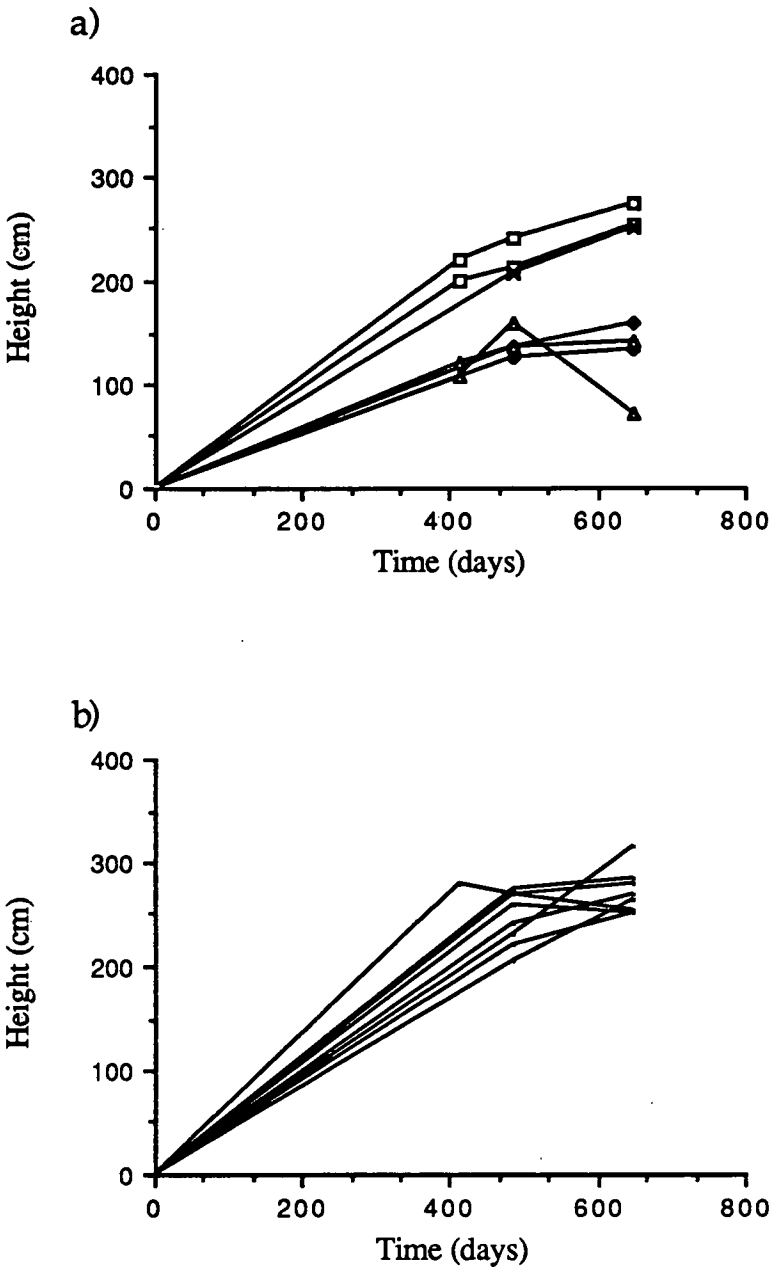


Figure 3.2 a) Height of individual breakaway stems after fire: Δ *Buchanania obovata*; ♦ *Erythrophleum chlorostachys*; □ *Eucalyptus miniata*; x *Eucalyptus tetrodonta*. b) *Acacia aulacocarpa*.

was 3 m H and two of the 38 saplings of this species survived the 1988 fire (Fig. 3.2).

3.3.2 Species growth patterns

Individuals of all species at each site were assigned to one of the following growth response categories:

1) All stems die to ground level in the second dry season. Stems resprout and the tallest stems exceed the height of the previous wet season.
2) As for 1, except resprouting stems do not attain the height of the previous wet season.
3) The height of the tallest stem declines in the second dry season but not all stems die back to ground level. Stems resprout and the tallest stem exceeds the height of the previous wet season.
4) As for 3, except resprouting stems do not attain the height of the previous wet season.
5) Stems die to ground level in the second dry season and do not re-emerge the following year.
6) The height of tallest stem does not decline throughout the sampling period.
7) Stem height is maintained following the initial post-fire episode until it declines in the second wet season.
8) Stem height remains constant following the initial post-fire growth episode.
9) Any pattern not included by the categories above.

Individual species favour specific response types ($P<0.001$; Table 3.1). The most common growth pattern for *Buchanania obovata*, *Terminalia ferdinandiana*, *Erythrophleum chlorostachys* and *Acacia aulacocarpa* is for the dominant stem to survive despite growth being slow (strategy 6). Stems of *Eucalyptus tetrodonta* and *Eucalyptus miniata* most commonly lose height through stem senescence after 1 year and do not regain that lost height by the end of the following wet season (strategy 4). The most common response of *Planchonia careya* and *Eucalyptus confertiflora* is to die back to ground level in the first dry season followed by replacement of above-ground biomass later in that season (strategy 1 and 2).

Table 3.1 Distribution of species x growth strategy. Strategies are defined in Section 3.3.2. Values are the observed/expected ratio. Expected values are derived from the proportion of each growth strategy for all species combined.

	Growth strategy									
Species	1	2	3	4	5	6	7	8	9	TOTAL
Buchanania obovata	0.15	0.00	0.40	1.18	0.00	1.87	1.74	0.00	1.76	47
Planchonia careya	3.02	1.48	0.96	0.28	0.00	0.35	1.43	3.75	0.00	44
Terminalia ferdinandiana	1.02	0.80	1.15	0.15	1.11	1.78	0.00	0.00	0.67	41
Erythrophleum chlorostachys	0.00	0.00	1.36	0.49	0.00	1.41	0.53	0.00	3.21	38
Eucalyptus confertiflora	2.59	3.48	1.23	0.66	1.25	0.00	0.53	0.00	0.00	38
Eucalyptus miniata	0.37	0.00	1.73	2.79	1.25	0.10	1.05	1.43	0.00	38
Eucalyptus tetrodonta	0.78	2.22	0.83	2.19	3.00	0.00	1.36	2.50	0.61	45
Acacia aulacocarpa	0.00	0.00	0.49	0.16	1.25	2.53	1.05	0.00	1.79	38
TOTAL	47	20	70	53	7	86	16	6	24	324

3.3.3 Comparisons between sites

Mean stem height is greater at A1 than at A4 for all of the six species occurring at both these sites (Fig. 3.1). Relative growth rate (R) was not significantly affected by the interaction of species and site ($P>0.05$). Comparison of R values for the combination of all measured species shows that growth is significantly greater at A1 than at A4 ($P<0.001$)(Table 3.2). Differences between sites are significant for *Buchanania obovata* ($P<0.01$) and *Erythrophleum chlorostachys* ($P<0.001$). The latter species grows slower at the site where it occupies the canopy layer. Other species do not have significantly different lignotuberous growth rates across the environmental range represented by this transect. For example, *Eucalyptus tetrodonta* has similar growth rates at the site where it dominates the canopy (site A2; Table 3.2) and where it occurs at the limits of its range in the forest-low forest ecotone (site A3; Table 3.2).

Table 3.2 ANOVA results of relative growth rate (R) differences between species and sites.

	Site									
	A1		A2		A3		A4		TOTAL	
Species	mean	n	mean	n	mean	n	mean	n	mean	F ratio
Buchanania obovata	3.75	19	NA	NA	NA	NA	2.51	20	3.11	8.60**
Planchonia careya	3.84	19	NA	NA	NA	NA	3.37	20	3.60	3.43
Terminalia ferdinandiana	3.91	17	NA	NA	NA	NA	3.81	23	3.85	1.62
Erythrophleum chlorostachys	4.33	19	NA	NA	NA	NA	3.11	21	3.69	2.20***
Eucalyptus confertiflora	3.03	16	NA	NA	NA	NA	2.65	20	2.82	5.52
Eucalyptus miniata	3.16	19	2.72	17	NA	NA	NA	NA	2.95	7.92
Eucalyptus tetrodonta	2.91	6	2.12	18	2.41	21	NA	NA	2.36	7.52
Acacia aulacocarpa	3.55	19	NA	NA	NA	NA	3.45	21	3.50	7.32
TOTAL	3.60	134	2.41a	35	2.41a	21	3.20	125		1.31***
F ratio	2.80**		2.29		NA		3.84**		7.35***	

* P<0.05, ** P<0.01, *** P<0.001; letters denote the sites not significantly different at P<0.05; NA not available
Significant differences between pairs of species are not shown.

3.3.4 Xylem pressure potential

The xylem pressure potential results can only be interpreted tentatively because of small sample sizes. Xylem pressure potential seems to be lower for the leaves of actively growing lignotuberous regrowth than for dormant lignotuberous stems (*Eucalyptus tetrodonta*; P<0.01, *Buchanania obovata*; P<0.05). Xylem pressure potential was not significantly different between the sites A1 and A4 for the standardized measurement that allowed the combination of species (P>0.05, n=25 and n=26 respectively). The results for *Eucalyptus confertiflora* are interesting because there is a reversal in the relative pressure potential values for the different lifeforms of this species across the gradient from forest to low forest (Table 3.3). Mean values are higher for lignotuberous stems than saplings in the low forest. Saplings have higher pressure potential values than lignotuberous plants in the forest. These relations were statistically significant in two of the four

Table 3.3 Mean values for xylem pressure potential (bars) and the significant differences between sites and lifeforms within species according to the Mann-Whitney U-test.

Species and lifeform	Site											
	A1			A2			A3			A4		
	mean	s.e.m.	n	mean	s.e.m.	n	mean	s.e.m.	n	mean	s.e.m.	n
Buchanania obovata												
old lignotuberous stem	112.0a	28.6	5	NA	NA	NA	NA	NA	NA	127.5a	16.0	4
Eucalyptus confertiflora												
old lignotuberous stem	223.6cd	15.7	7	NA	NA	NA	NA	NA	NA	282.8b	7.9	9
sapling	258.1bce	22.1	8	NA	NA	NA	NA	NA	NA	195.0de	21.1	8
Eucalyptus tetrodonta												
young lignotuberous stem	270.0f	15.6	3	240.0f	8.9	7	252.0f	16.2	5	NA	NA	NA
old lignotuberous stem	NA	NA	NA	NA	NA	NA	391.4	18.0	7	NA	NA	NA

Letters denote pairs, between sites and lifeforms, not significantly different at $P<0.05$. NA- not available.

comparisons of lifeform and site ($P<0.01$) despite the small sample sizes (Table 3.3).

3.3.5 Response to fertilizer

The height and number of stems were not significantly different for any species between burnt, fertilized; unburnt, fertilized and unburnt, unfertilized treatments ($P>0.045$ in all cases).

3.3.6 Clipping versus burning

The height and number of stems were not significantly different for any species between the clipped and burnt treatments ($P>0.045$ for all cases).

3.3.7 Mature tree growth

The annual growth rates of the species varies between mean values of 0.1 to 3.9 mm dbh annual increment (Table 3.4). With the exception of the indeterminant patterns of *Planchonia careya*, all species exhibit the greatest girth increase during the wet season (Fig. 3.3). The girth of most species declines during the dry season.

Table 3.4 Mean initial diameter (and s.e.m.) and mean annual diameter increment (and s.e.m.) of open forest trees.

Species	Initial diameter (mm)		Annual diameter increment (mm)	
	mean	s.e.m.	mean	s.e.m.
Buchanania obovata	89.3	16.8	1.5	0.4
Planchonia careya	92.7	9.4	-0.3	0.2
Terminalia ferdinandiana	86.5	7.8	0.8	0.4
Erythrophleum chlorostachys	200.4	28.4	1.6	0.4
Eucalyptus confertiflora	142.7	19.8	0.5	0.3
Eucalyptus miniata	205.9	26.6	2.0	0.5
Eucalyptus tetrodonta	204.1	30.6	2.9	0.6
Acacia aulacocarpa	112.4	14.9	1.7	0.8

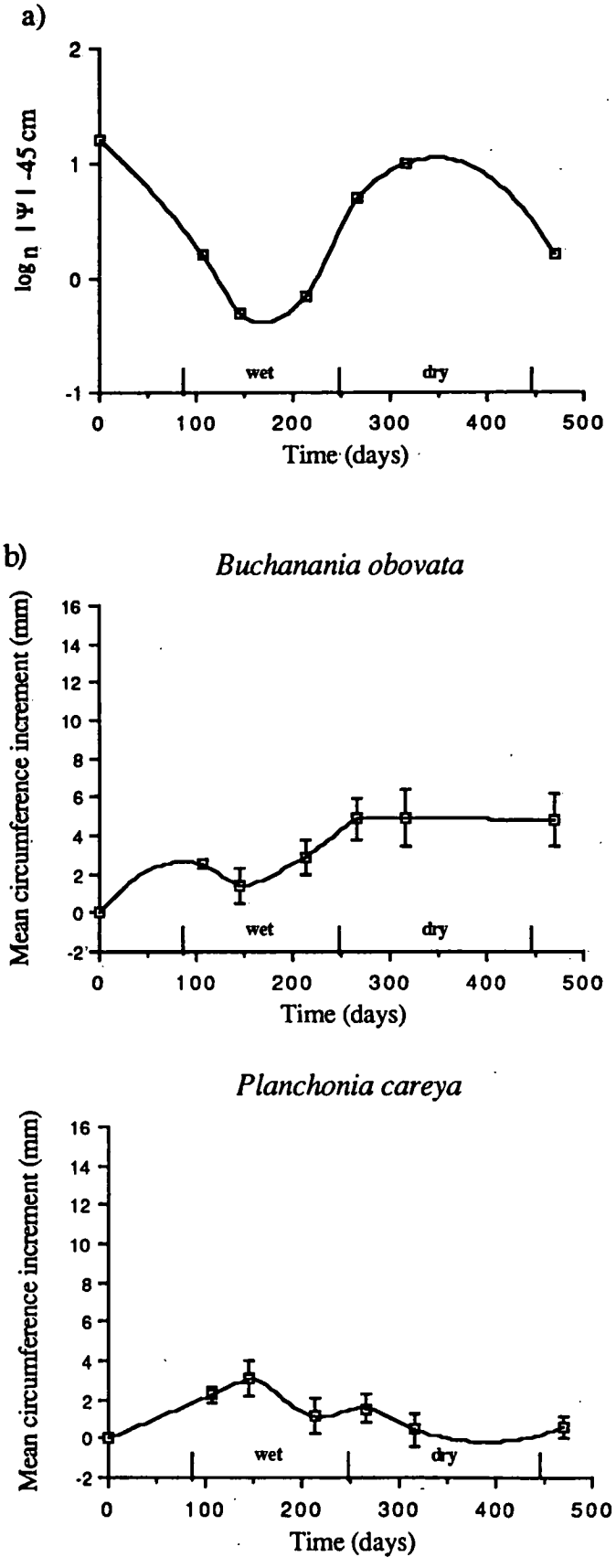


Figure 3.3 a) Seasonal matric potential (Ψ) cycle at 45 cm at the site of mature tree growth measurement. b) Mean circumference increment (and s.e.m.) of eight trees.

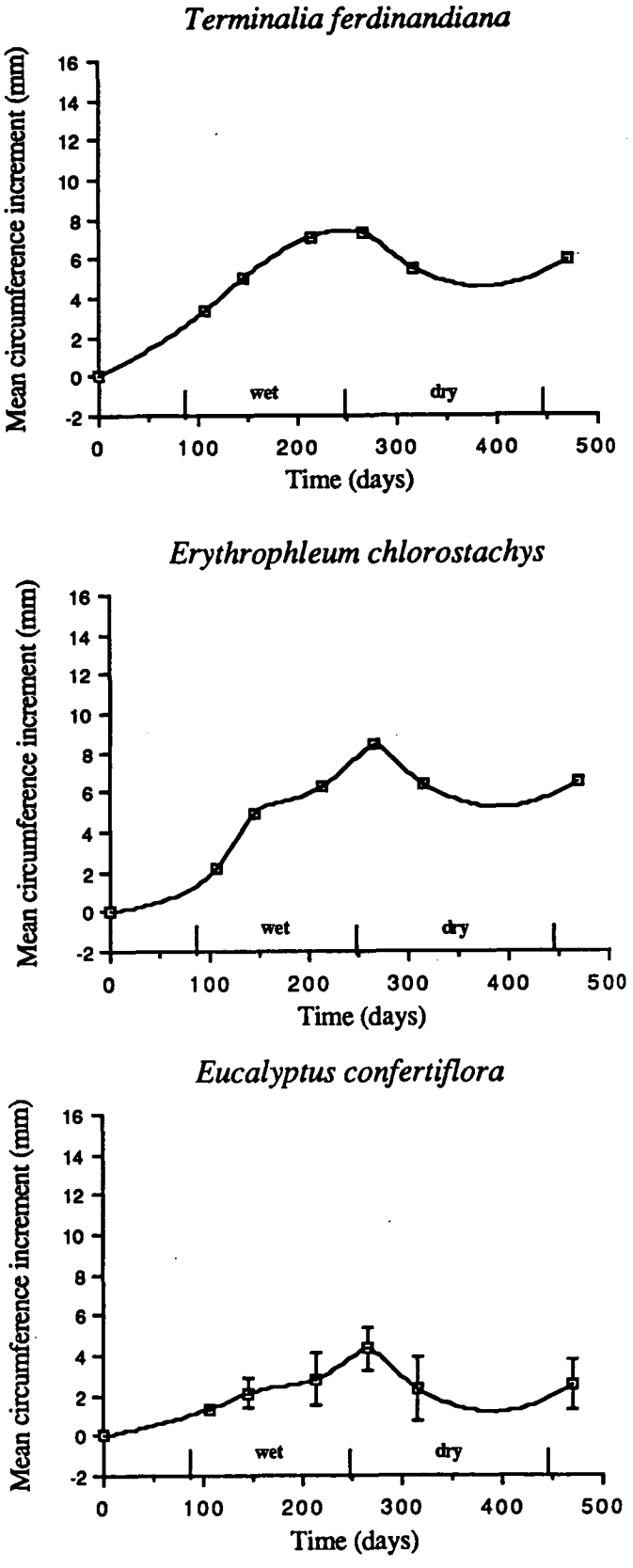


Figure 3.3 b) continued

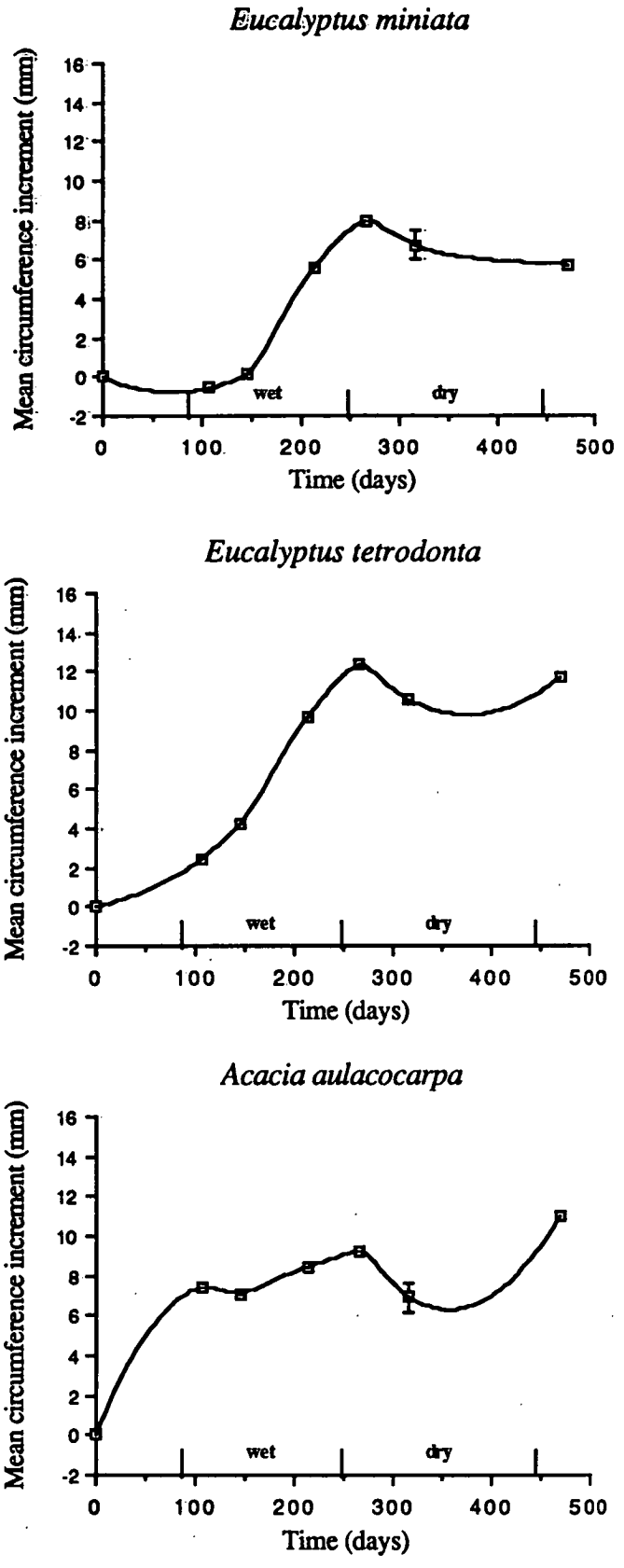


Figure 3.3 b) continued

3.4 Discussion

Several authors note that young trees of tropical forest show more continuous growth than the patterns exhibited by older trees whose extension growth commonly occurs in short bursts (Njoku 1964, Borchert 1978). In tropical savanna forest of Australia, it is apparent that the growth of trees involves more than two phases. Underground woody organs with short annual stems are a prominent and longlived lifeform in this part of the world and they seem to have a growth strategy that is distinct from either saplings or mature trees. The vast majority of woody sprouts have lengthy periods of dormancy that preclude their chances of reaching sapling size before the next fire. It is difficult to obtain information on the growth of individuals that leave the ground layer and become saplings because of their low densities. However, for the few saplings monitored in this study it seemed that once they attained 2 m H their growth becomes more continuous than stunted ground layer stems (cf. Figs. 3.1 and Fig. 3.2). This is most evident for the overstorey trees *Eucalyptus miniata* and *Eucalyptus tetrodonta*. Despite their more continuous growth, no saplings attained sufficient height to survive a fire two years after emergence.

There is now a significant body of measurements of cambial and shoot extension of mature trees from the forest (Njoku 1963, Alvim 1964, Hopkins 1970a, Daubenmire 1972, Frankie *et al.* 1974, Huxley and van Eck 1974, Alvim and Alvim 1978) and savanna (Boaler 1963, Jeffers and Boaler 1966, Hopkins 1970b, Monasterio and Sarmiento 1976) of the seasonal tropics. All these studies show that the growth patterns of individual trees varies widely. Daubenmire (1972) found that cambial growth usually follows shoot extension and may be delayed up to several months. Tomlinson and Gill (1973) suggest that radial and extension growth in the tropics occur independently. Extension and cambial growth can occur in any season although the leafless period for deciduous species is invariably during the dry season. Leaf flushing may occur more than once in a season. It may be continuous or can occur in seasonal bursts. A common situation for both deciduous and evergreen tropical trees is a growth flush before the onset of rains in seasonal tropical climates. It is rare for seasonal shoot growth to occur continuously through the rainy season when growing conditions are

apparently most favourable. In many instances it is not possible to correlate shoot extension growth and leaf flushing with environmental factors and there is a stream of opinion that places increasing importance on endogenous factors for initiation of growth (Greathouse *et al.* 1971, Borchert 1973, Huxley and van Eck 1974). Hopkins (1970a) found that intraspecific differences are greater than seasonally consistent changes.

While most of the mature trees measured in this study undergo cambial expansion during the wet season, the timing of shoot extension growth is less clear and was not systematically quantified in this study. However, observations made during the course of two years continuous field study in tropical eucalypt forest verify the observations of Kerle (1985) and Specht (field notes; reported in Specht and Brouwer 1975) that trees are frequently flushing in the late dry season. *Terminalia ferdinandiana* breaks its dormant deciduous phase before increases in soil moisture with the arrival of the wet season (noted on the 1/9/87 by the author). Russell-Smith (1986) measured seasonal changes in xylem pressure potential of tropical trees in a range of north Australian vegetation types. He was surprised to find that *Erythrophleum chlorostachys* was less stressed in the latter half of the dry season when soil conditions are more xeric than in the mid-dry season. He noted that the late dry season coincides with a period of leaf flush in this species. The new leaves of this species are particularly obvious by virtue of their lighter shade and are most prominent during the driest period (from July to September) on Melville Island.

Sarmiento *et al.* (1985) verify that most tree species of neotropical savanna renew their foliage during the dry season when moisture conditions are least favourable. Furthermore, they showed that leaf water potential shows little seasonal variation. These results seem to verify the conclusions of Medina (1982) and Goldstein and Sarmiento (1987) that the growth of tropical trees is not limited by seasonal drought. Chapter 2 provides evidence that surface soil moisture is rarely beyond wilting point and that moisture conditions at depth are favourable all year round under most Melville Island forests. If downward growth is not inhibited by heavy soil the root systems of the savanna trees are able to access moisture reserves.

Dry season extension growth in mature trees cannot be explained by the reallocation of moisture reserves from non-photosynthetic plant organs. Although trunk shrinkage is common for tree species in northern Australia (Fig. 3.3, Werner 1986) and throughout the seasonal tropics (Boaler 1963, Hopkins 1970a, Daubenmire 1972, Alvim and Alvim 1978) the reallocation of water within the plant could not meet a fraction of the transpiration demand. Foldats and Rutkis (1975) calculate this demand as 67 l/day for a 3.5 m tree in the Venezualan savanna. Furthermore, trunk shrinkage is particularly evident during the first half of the dry season when deciduous and semi-deciduous trees are losing leaves. This relationship has been observed elsewhere by Daubenmire (1972). Sarmiento *et al.* (1985) have suggested that a constant level of stomatal conductivity is necessary for the maintenance of the internal carbon balance and the perpetuation of nutrient cycling within the plant. Monasterio and Sarmiento (1976) have suggested the wet season is a period of photosynthetic activity and the replacement of the assimilatory system occurs during other periods.

It is interesting that the annual growth of woody stems in the ground layer following a fire coincides with warming temperatures (Fig. 3.4). Dunlop (1988) has suggested that this slight rise in temperatures precipitates a "northern spring" whereby growth occurs despite the dry conditions. Ferrar *et al.* (1989) provide some evidence that the photosynthetic rate of *Eucalyptus miniata* declines rapidly in response to decreased temperatures. Unfortunately the critical acclimation period and its relationship to dry season diurnal temperature fluctuations is unknown. It is difficult to imagine the adaptive significance of synchronizing growth with temperature rise in a climate where annual fluctuations are slight and minimum temperatures during the coldest months are far higher than those of the temperate region where the spring growth phenomenon is a reality. It is conceivable that slight temperature or photoperiod changes provide an environmental cue that stimulates plant growth during periods that are optimal in relation to some other factor. Both temperature and photoperiod have been shown to stimulate growth of tropical trees under controlled conditions (see Longman 1978).

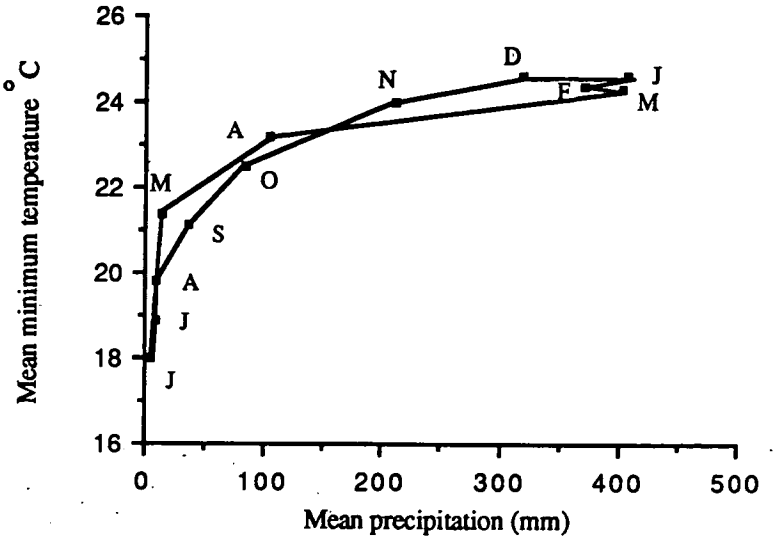


Figure 3.4 Hythergraph, Pularumpi, Melville Island. Months are annotated.

It has been emphasized that the ability to refoliate is an adaptation of the Australian woody flora to fire (Gill 1981, Hodgkinson and Griffin 1982). Many plants maintain reserves in non-photosynthetic organs that can be utilized following a defoliation event. Thus, growth of woody sprouts in the late dry season may simply be a response to the destructive effect of fire, as has been shown for lignotuberous plants in African savannas (Hopkins 1963). Comparison of clipped and burnt treatments suggests that the growth response of ground layer trees is not inhibited or enhanced by fire but is simply a response to defoliation.

When ground layer stems are fire protected their growth in the following year although slight seems to coincide with the arrival of rain rather than rising temperatures. The relationship between growth and the seasonal environment could be further tested in relation to woody sprouts by comparing growth following the severing of stems at different times of the year.

As for mature trees, the growth of woody sprouts does not seem to occur in concert with available soil moisture. The seemingly universal phenomenon whereby growth of emergent woody sprouts declines in coincidence with the arrival of wet season rain and rising soil moistures is particularly enigmatic.

Growth is not limited by excess water as the forest is usually associated with deep free draining red earths and the water table does not approach the surface in a typical wet season (Chapter 2).

Soil fertility was not measured, so it cannot definitely be established that the fertilizer trial increased the amount of nutrients available to the root systems of the woody sprouts. However, it is worth noting that native tree seedlings responded very strongly to fertilizer in an experiment on Melville Island (Wilson 1990). The quantities of fertilizer per plant were much lower than those applied in the fertilizer trial presented here (Section 3.2.3). The non-response of woody sprouts to increased nutrient conditions is verified by other work of Wilson (1990), where *Eucalyptus tetrodonta* root suckers did not respond significantly to fertilizing. From this evidence it seems that the growth of woody sprouts is not limited by soil macronutrients.

Sarmiento *et al.* (1985) suggest that nutrient loss by leaching from leaf surfaces has selected against a wet season growth strategy. Subsequent chapters of this thesis examine other possible explanations for growth suppression. Chapter 5 examines the possibility that the eucalypt overstorey inhibits regeneration in these forests. Another possibility is that stems are suppressed by herbivory. It was evident during the course of this study that the leaves and stems of the woody sprouts were suffering considerable insect damage. Chapter 6 examines the possibility that growth in the ground layer of the eucalypt savanna forest is tuned to avoid insect herbivory.

The enigma of limited growth may be a conceptual problem based on the presumption that individuals in the ground layer seek to realize their potential as trees. A lifeform whereby growth occurs only in response to defoliation may be an efficient alternative to the tree form. Investing in growth may be maladaptive when the chance of reaching

the overstorey is limited by frequent fires. Photosynthates produced during the dormant period may be translocated to underground parts where they can be more efficiently utilized than by stems. The lignotuberous alternative is particularly viable for the most common broadleaved species of the open forest, *Buchanania obovata*, *Planchonia careya* and *Terminalia ferdinandiana*, that have the capacity to flower and set fruit before the following fire season (Plate 3.1). Sarmiento and Monasterio (1983) note that the ability to set seed on annual stems is a common feature of trees in the savanna environment. For other species that are only sexually mature as trees, the accession from ground layer to tree may only have to occur at low frequencies to ensure their perpetuation.

Growth rate and stem height of all species was greater in the forest than the low forest. Slow growth in the low forest is consistent with evidence from Chapter 2 which suggests that heavy soils under this vegetation type are less favourable than the deep sandy loams supporting forest. The propensity to occupy the upper canopy was not reflected by species growth rates. *Erythrophleum chlorostachys*, *Terminalia ferdinandiana* and *Eucalyptus confertiflora* are common as canopy trees in the low forest but rarely so in the forest. On this basis it is difficult to explain the relatively slow growth of these species in the low forest. The demographic structure of the individuals in the ground layer of the low forest may represent cohorts that are physiologically unsuitable for rapid growth (see Section 5.3.5). However, this is an unlikely explanation for slow growth rates in the low forest because the ground layer populations appeared multi-aged as indicated by their range of sizes. The structural development of the dominant broadleaved trees in the low forest may be favoured by the absence of tall evergreen eucalypts. Species such as *Eucalyptus miniata*, *Eucalyptus nesophila* and *Eucalyptus tetrodonta* are probably excluded by the heavy soils under the low forest. In the forests that these evergreen species dominate, the development of other species seems limited. However, the analysis of growth rates presented in this study suggests that an inhibitory mechanism does not operate in the early stages of regrowth, where woody sprouts exhibit an annual pattern of regeneration followed by limited growth. It may be that the critical phase is the switch from this lifeform to sapling. The probability of

Plate 3.1 One year old lignotuberous stem of *Buchanania obovata* with fruit.

this switch occurring may be lowered in situations where the evergreen trees have a stronghold. The plot areas and time frames used in this experiment were inadequate for observing the process whereby ground layer stems become saplings.

The growth strategies of the woody sprouts suggests that the vast majority of individuals are incapable of attaining, or have developed a viable alternative to, the tree lifeform in the tropical eucalypt forest. This suggestion raises further interesting questions regarding the switch from woody sprout to tree habit? Is this switch determined by the physiology of the plant? Is the switch genetically predetermined? What are the influences of environmental triggers? These questions will have to be answered before the regeneration process of tropical eucalypt forest is clearly understood.

CHAPTER 4 INTERACTIVE EFFECTS OF FIRE AND SITE FACTORS IN TROPICAL EUCALYPT FOREST

4.1 Introduction

4.1.1 Background

The response of tropical savanna vegetation to fire exclusion is not consistent between the continents. San Jose and Farinas (1983) present evidence from Venezuala indicating that long periods of fire exclusion result in a progression from open savanna to a forest physiognomy. This transition is a result of the development of savanna tree species rather than the invasion of forest species. This conclusion is verified from descriptions of other South American fire exclusion experiments (Eiten 1972, Coutinho 1982). The most extensive set of fire exclusion experiments have been established in western Africa where it seems that fire is necessary for the maintenance of the savanna (Ross-Innes 1972). Results show that succession towards a climax vegetation which is ultimately akin to closed forest and floristically distinct from the original vegetation, will occur. Bowman *et al.* (1988a) found no evidence for this shift following 13 years of fire exclusion in eucalypt savanna forest and woodland at Munmalary in monsoonal Australia. The closed monsoon forest is floristically distinct from the more open vegetation formations in tropical Australia (Taylor and Dunlop 1985) and few if any species from the closed forest formations were present following fire protection at Munmalary.

Because there is little evidence of succession fire ecology research in monsoonal Australia has focused on the influence of fire on structure and dominance within the savanna system. Braithwaite and Estbergs (1985) describe the size class distribution of some savanna tree species and suggest that poor representation of some species in the mid and higher canopy layers indicates that the timing and frequency of fire may be critical in allowing the breakaway of these species from the ground layer. Following fire protection at Munmalary structural changes did occur although the species that entered the midstorey were short lived trees and shrubs (*Acacia* sp.), the exception was *Erythrophleum chlorostachys* in the forest and two broadleaved species

in the woodland. The Munmalary experiment required large amounts of money and energy to maintain and the fire protected vegetation bears little resemblance to shrubby open forests that occur in natural situations. Bowman and Dunlop (1986) and Wilson and Bowman (1987) describe north Australian formations with a midstorey of broadleaved shrubs. These authors postulate that this vegetation type has characteristics that are intermediate between grassy open forests and monsoon forest. If the probability of ignition were equal for all areas the abundance of grass would be the major determinant of fire frequency in Top End vegetation (Bowman and Wilson 1988). The communities with broadleaved midstoreys usually have less grass, are burnt less often and may have some floristic relation to monsoon forest. Occasionally these shrubby formations include species that are rarely found away from thicket but more usually these formations have their understoreys filled with the broadleaved species that are normally present as stunted woody sprouts in the grassy forests. Bowman (1988) has suggested that some of the shrubby eucalypt forests are a result of the interaction between greater growth rate and lower fire frequency on sites where water can be accessed through the dry season. He suggests that favourable dry season moisture conditions are exploited by shrubby species and they attain sufficient height to avoid destruction of their above-ground parts by less frequent fires.

The Munmalary evidence suggests that relief from fire does not contribute to the probability of a regeneration event. The fact that saplings of the dominant eucalypt species were no more frequent in the unburnt forest suggests that the stocking of these forests is limited by some factor other than fire. The previous chapter showed that even with relief from fire the growth of woody sprouts in the ground layer of the eucalypt forest is suppressed and that the development of saplings is an extremely low frequency event.

Fire is a high probability phenomenon in the eucalypt vegetation of the Top End and is usually an annual occurrence (Press 1988). Because of this fact the opportunities to study the effects of fire exclusion are rare. The active exclusion of fire from a property near Humpty Doo provides such an opportunity in similar vegetation to forest at Munmalary and Melville Island but in a different geomorphic

environment. This study addresses the hypothesis that the promotion of tree regeneration is influenced by edaphic controls.

4.1.2 Site history

The Solar Village is 120 ha of cooperatively owned bush land about 35 kilometres southeast of Darwin in the Northern Territory (Fig. 4.1). Houses have been constructed on the property and small gardens established although the general ethos of the community is directed towards preserving their bush in an undisturbed condition. Since 1978 the property has been protected from fire. The recent fire history of the surrounding country was determined by discussions with the owners, one of whom has kept notes on the timing and intensity of fires that have burnt the surrounds of the Solar Village. The bush to the south of the property is burnt annually by fires that are swept to a boundary fire break by south east winds. The land between the strip mining area and the Solar Village is afforded protection from fire to the east and west (Fig. 4.1). Consequently it is not burnt annually (four fires from 1980-1988) and when burning does occur it is generally by the cooler flanks of southeasterly fanned fires. The field work was carried out after this western strip had been burnt in the previous dry season by a cool evening fire following at least five years of fire exclusion.

The densities of agile wallaby (*Macropus agilis*) are extraordinarily high within and around the Solar Village property and they may recognise the area as a secure refuge from the hunter's gun. However, there is no reason to assume that grazing is more intense within the Solar Village than the immediate surrounds as there are no fences defining the limits of the animals' safe haven.

The low ridge running northwest across the southwest corner of the property was chosen for study as an examination of pre-1978 aerial photos and of the geomorphic environment suggested that this was the most uniform environment where comparisons between fire histories within one vegetation type were possible.

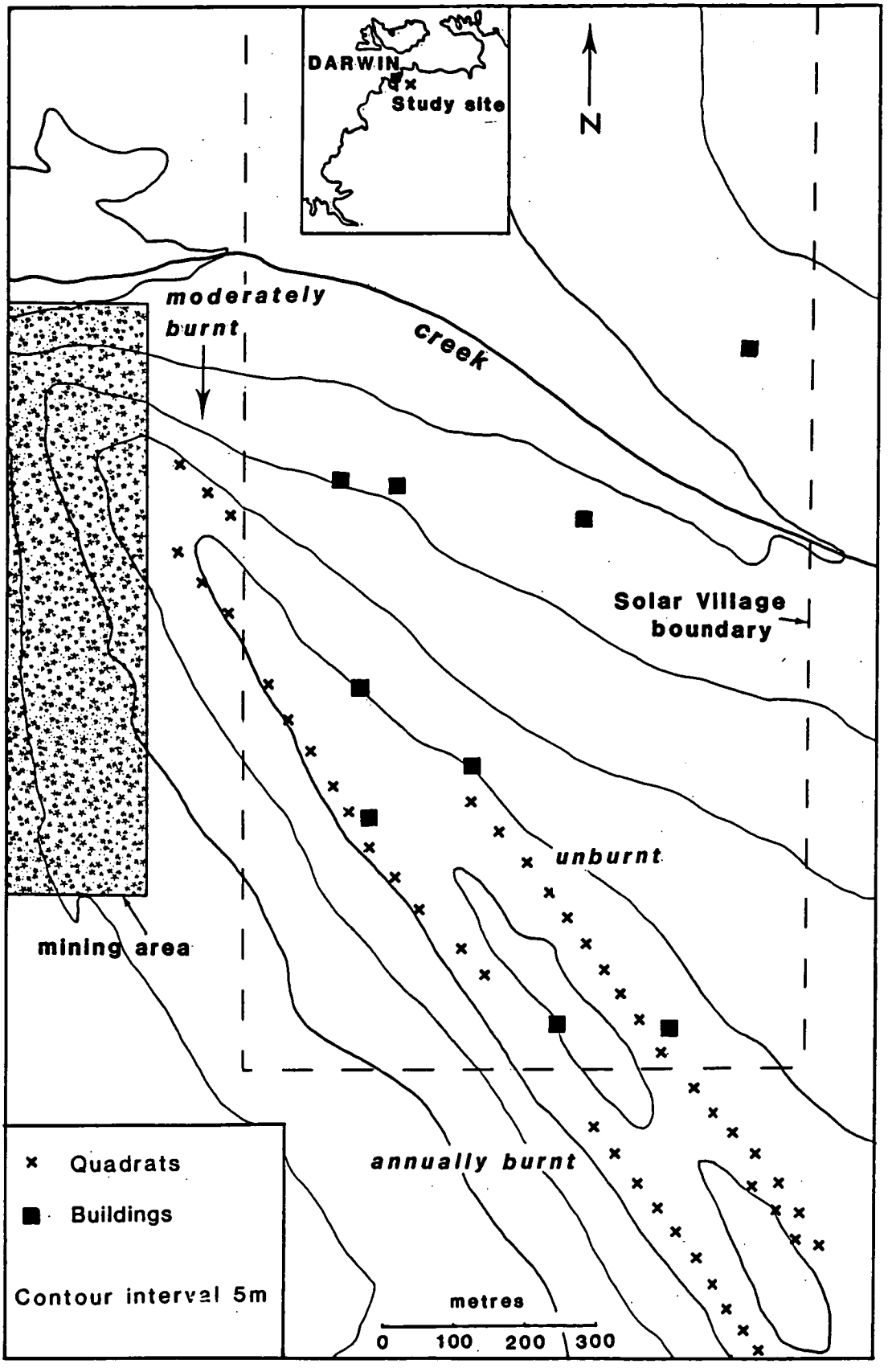


Figure 4.1 Location map showing the boundary of the fire protected Solar Village, the topography of the site and the location of buildings and quadrats

4.1.3 Physical environment

The rocks of the sampled site form a strike ridge and are part of the Acacia Gap Formation which is comprised of medium to coarse grained sedimentary rocks, including sandstone, siltstone and greywacke, all of which have undergone various types of metamorphosis (Pietsch and Stuart-Smith 1987). The soils are very rocky, poorly differentiated, grey brown sandy loams. The forest is dominated by *Eucalyptus miniata* and *Eucalyptus tetrodonta*. These tree species and others including acacias, the tree legume *Erythrophleum chlorostachys* and broadleaved species such as *Terminalia ferdinandiana, Buchanania obovata, Planchonia careya* and *Xanthostemon paradoxus* are common members of the ground layer and regenerate from underground organs after fire. The ground layer is dominated by a sparse cover of grasses whose dominants flower progressively from September to April in the following order, *Alloteropsis semialata, Eriachne avenacea, Chrysopogon fallax, Sorghum intrans, Heteropogon triticeus* and *Pseudopogonatherum contortum*.

4.2 Methods

4.2.1 Sampling procedure

Forty-six plots were spaced around the contours of both flanks of the ridge (Fig. 4.1). The sampling procedure almost entirely mimics that of Bowman *et al.* (1988a) and was carried out in March 1988. All higher plants were recorded within 10 x 10 m plots according to a six point cover abundance scale (+ (barely present), <5%, 6- 10%, 11- 25%, 25-50%, >50%) that is more sensitive to low abundances than the Braun-Blanquet scale. The density and dbh of saplings (>3 m high but <10 cm dbh) within the plot was determined. The Bitterlich variable plot method (wedge factor = 0.7) was used to determine the abundance and basal area of the overstorey species using the centre of the plot as the turning point (Mueller-Dombois and Ellenberg 1974). Woody sprouts <3 m tall were counted within a 1 m strip around the perimeter of the quadrat. Plant species nomenclature follows Dunlop (1987) and collections of undescribed species are held in the Darwin Herbarium.

The percent cover of grass, rock and litter were estimated. During June 1988 surface soil samples were taken by scraping away 1 cm of surface soil and sealing a trowel full of the exposed soil in a jar. Gravimetric moisture (according to Curtis and Trudgill 1974), rock content and field texture were determined. Soil colour was examined using Munsell Charts.

4.2.2 Analytical methods

All data were stored on DECODA (previously ECOPAK Minchin 1986) which contains the non-metric multidimensional scaling ordinating technique KYST. While this program has been shown to be the most robust of available ordination techniques (Minchin 1987), it demands a considerable computing resource and was used here on species presence-absence in two, three and four dimensions with ten starts, one of which had a starting configuration defined by the ordination scores of another less demanding ordination technique, detrended correspondence analysis (DECORANA; Hill 1979a). Further ordinations to search for patterns within fire histories were performed using DECORANA. Overstorey trees, saplings and woody sprouts were considered as separate species and according to their grouping as eucalypt, acacia, *Erythrophleum*, cycad or broadleaved tree. The normality of the following variables was tested prior to two-way ANOVA (fire history and aspect as sample groups): environmental variables, species richness, individual species (using the mid-points of the abundance categories of species occurring in six or more quadrats), overstorey basal area and the abundance of saplings and woody sprouts. Some variables measured on an integer scale required no transformation although most were satisfactorily improved by the $\log_{10}(x+1)$ transformation. Most species population distributions as measured by the ordinal abundance scale required a square root transformation. Exploratory analysis revealed many species that had significantly different responses between the southern area subject to hot annual fires and the six plots in the lightly burnt area to the west. Thus they were treated separately and will be referred to as the annual and moderately fired histories. Two-way ANOVA was used to test the significance of fire and aspect. The Student-Newman-Kuels multiple range test was used to test the difference between each pair of fire

histories where fire was a significant main effect.

Relations between ordination scores and environmental variables were explored using Pearson's product moment correlation coefficient.

4.3 Results

4.3.1 Environmental determinants of vegetation gradients

The burnt and unburnt plots are clearly divided across the primary axis of the ordination space (Fig. 4.2). The split does not appear to be a function of an unforeseen gradient running along the ridge as there was no statistically significant correlation between first, second or third axis DECORANA scores (following ordination within fire history blocks) and distance along the ridge ($P>0.05$). The importance of fire in affecting floristic change is ratified by the ANOVA of first axis ordination scores by fire history ($P<0.001$).

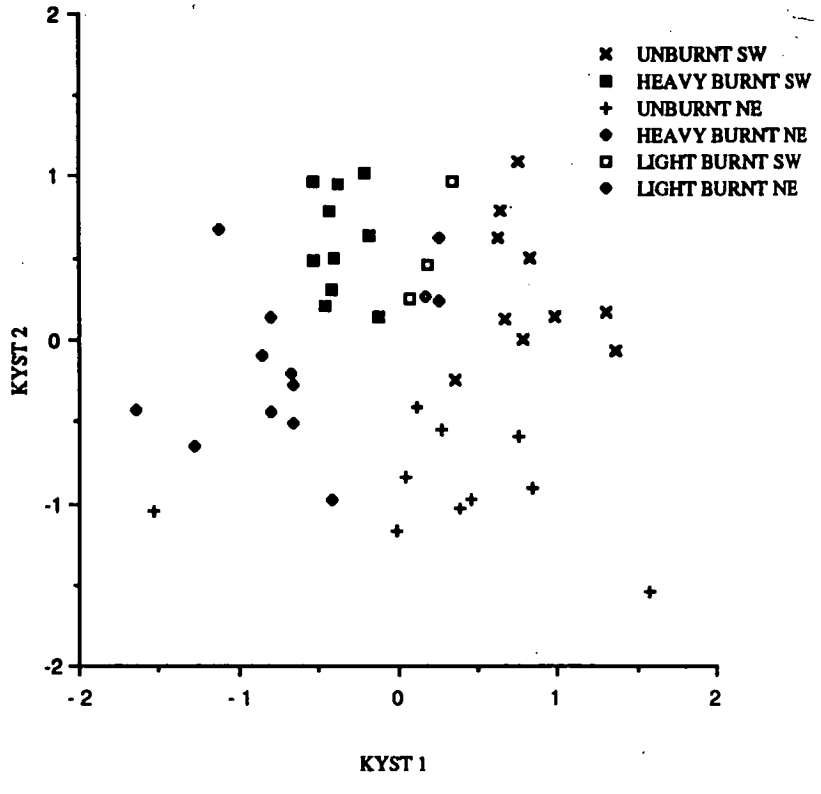


Figure 4.2 Two-dimensional KYST result with quadrats designated according to their fire history and aspect.

The second axis of the KYST ordination is clearly reflects the aspect of the ridge faces ($P<0.001$)(Fig. 4.2) and the nature of this influence requires discussion. The substrate of the site is large rocks in a skeletal soil matrix with smaller fragments of rock and gravel. The gravimetric soil moisture term can be considered as the percentage of water in the whole soil sample or as a proportion of the gravel free portion of the sample. In rocky or gravelly soils these are substantially different.

There are statistically significant differences between measures of surface rockiness and soil moisture (Table 4.1 and 4.2). The southwesterly aspect of the ridge has significantly greater surface rock than the northeasterly face. Kirkpatrick *et al.* (1988) studied the influence of aspect on the vegetation of a hemispherical hill with steeper slopes than the Solar Village ridge. They concluded that decreased available soil moisture resulting from greater insolation loads on northern than southern aspects was the primary cause of vegetation patterns. They showed that insolation differences between north and south aspects are greatest during June, the time of soil moisture determination at the Solar Village. If this phenomenon was the cause of the aspect effect at the Solar Village then the southwest face should be drier than the northeast. This cannot be statistically verified. In fact Table 4.2 indicates that the inter-rock soil with annual fire and fire exclusion (the most effectively sampled fire histories) is moister on the northeastern face. Both measures of soil moisture were strongly correlated with KYST axis 2 (Fig. 4.2)($P<0.001$). The aspect effect may reflect edaphic factors resulting from geomorphic differences in the nature of the sedimentary substrate on the two ridge faces.

Whatever the cause of aspect separation on the ordination space the clear distinction necessitates the consideration of the two faces of the ridge as stratified sample groups of the three fire history groups. There were no obvious differences in the physical characteristics of the surface soils between fire histories or aspect. All the samples were sandy loams of uniform colour.

Table 4.1 Two-way ANOVA results showing mean scores for environmental variables and the significance of fire and aspect effects; and the significance of fire-aspect interactions.

	Fire history				Aspect			Fire x Aspect
Environmental variable	No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n=23)	F value	F value
Rock cover (%)					31.4	20.9	7.46***	N.S.
Gravel (%)		N.S.		NS		N.S.	N.S.	N.S.
Water in total sample (%)	2.6a	2.2ab	2.2b	3.5*				
Water in soil (%)								5.60***
Litter cover (%)	83.3	32.5a	21.8a	27.41****	55.4	44.4	4.87*	N.S.
Grass cover (%)	31.5a	52.5ab	60.0b	10.69****	51.1	42.2	4.24*	N.S.

**** P<0.001, *** P<0.01, **P<0.02, * P<0.05, NS P>0.05
N.S.- not significant at the 0.05 level
letters denote means not significantly different at P<0.05

Table 4.2 Mean (and s.e.m.) percentage moisture in soil according to fire history and aspect.

	South		North	
	mean	s.e.m.	mean	s.e.m.
No fire	4.53	0.28	7.10	0.55
Moderate	5.23	0.63	3.87	0.81
Annual	4.70	0.28	5.59	0.47

4.3.2. Fire and aspect effects on species composition

Species richness per 100 m^2 was significantly greater on moderately and annually burnt sites (Table 4.3). Thirty six of the 69 frequent species were significantly affected by fire history, regardless of aspect, as measured by their cover abundance (Table 4.4).

Table 4.3 Two-way ANOVA results showing effects of fire history, aspect and their interaction on species richness (species per 100 m^2).

Fire history				Aspect			Fire x Aspect
No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n=23)	F value	F value
35.5	41.2a	39.3a	9.19****	39.5	36.3	9.19***	NS

**** P<0.001, *** P<0.01, ** P<0.02, * P<0.05, NS P>0.05
letters denote pairs not significantly different at P<0.05

Thirteen herbaceous species showed statistically significant response to fire, regardless of aspect. All but one of these species had their highest mean abundance on annually or moderately burnt sites (Table 4.4). Many of the herbaceous peas that are prominent and diverse in the understoreys of Top End eucalypt forests were favoured by regular burning. This may relate to the heat requirement of many Australian legume seeds prior to germination (Purdie 1977, Warcup 1980, Mayer and Poljakoff-Mayber 1982 p 53).

Twenty-nine of the 69 frequent species were significantly affected by aspect and these are listed with their aspect preferences in Table 4.4.

Table 4.4 Two-way ANOVA results showing effects of fire history, aspect and their interaction on the percentage cover of higher plant species.

		Fire history				Aspect			Fire x aspect
Plant species	Lifeform	No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n = 23)	F value	F value
Crotolaria medicaginea	p/h/a	1.30	3.3a	2.5a	12.53****			NS	NS
Crotolaria montana	p/h/a	0.70	3.3a	2.1a	10.34****			NS	NS
Polygala eriocephala	h/a	0.60	2.5a	1.6a	8.24****			NS	NS
Thaumastachloa major	g/a	0.60	4.2a	4.4a	7.43***			NS	NS
Commelina lanceolata	h	0.6a	1.3ab	1.6b	6.21***			NS	NS
Heteropogon triticeus	g	11.0a	24.2ab	20.4b	4.15*			NS	NS
Spermacoce brevifolia	h/a	1.5a	2.0ab	2.5b	3.58*			NS	NS
Sorghum intrans	g/a	6.0a	6.3a	34.50	27.38****			NS	NS
Helicteres dentata	h	0.1a	0.0a	1.40	16.11****	0.30	1.00	7.07**	NS
Eriachne avenacea	g	2.0a	0.0a	8.40	11.67****	1.50	7.50	21.01****	NS
Phyllanthus simplex	h	0.0a	0.4ab	0.9b	7.23***			NS	NS
Eriosema chinense	p/h	0.1a	0.0ab	0.9b	4.61**			NS	NS
Polygala sp. RJF 682	h/a	0.10	0.4ab	0.9b	3.61*			NS	NS
Austrodolichos errabundus	p/v	0.0a	2.50	0.0a	37.3****			NS	NS
Pseudopogonantherum contortum	g/a	0.40	14.20	2.80	21.88****			NS	NS
Cochlospermum fraseri	t	0.0a	10.80	0.4a	20.03****			NS	NS
Eucalyptus porrecta	t	2.5a	14.60	1.4a	7.86****			NS	NS
Breynia cernua	t	1.4a	7.90	0.3a	5.40***	3.30	0.20	6.80**	NS
Flemingia parviflora	p/h	4.5a	8.30	3.0a	4.44**			NS	NS
Cassia mimosoides	p/h/a	1.0a	0.0ab	0.9b	4.44**			NS	NS
Elephantosus scaber	h	1.6ab	2.5a	0.6b	5.94**	1.90	0.80	5.93**	NS
Polygala orbicularis	h/a	1.6a	2.5a	0.80	6.48***			NS	NS
Ipomoea gracilis	v	1.2a	0.9ab	0.1b	5.07**			NS	NS
Xanthostemon paradoxus	t	13.9a	14.2ab	1.1b	6.17*	12.50	4.20	5.77*	NS
Urena lobata	h/a	0.6a	0.8ab	0.0b	4.27*			NS	NS
Acacia aulacocarpa	t	8.00	1.7a	1.0a	8.64****			NS	NS
Acacia leptocarpa	t	1.8a	0.0ab	0.0b	5.12***			NS	NS
Hibbertia sp. RJF 672	s/s	7.5a	4.2ab	3.5b	4.85**			NS	NS
Chrysopogon fallax	g				NS	20.00	3.20	27.32****	NS

Table 4.4 continued

Plant species	Lifeform	Fire history				Aspect			Fire x aspect
		No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n = 23)	F value	F value
Terminalia ferdinandiana	t				NS	28.30	9.00	25.70****	NS
Tacca leontopetaloides	h				NS	2.20	0.90	22.66****	NS
Calogyne holtzeana	h/a				NS	0.00	1.00	18.67****	NS
Ampelocissus acetosa	v				NS	6.50	3.70	10.71***	NS
Clerodendron floribundum	t				NS	2.40	0.70	10.32***	NS
Ipomoea graminea	v				NS	1.40	0.60	6.23**	NS
Scleria brownii	gm				NS	0.90	0.20	5.37*	NS
Vigna lanceolata	p/v				NS	1.80	0.90	4.11*	NS
Pachynema sphenandrum	h				NS	0.00	0.70	11.69****	NS
Acacia mimula	t				NS	2.00	5.70	7.46***	NS
Sauropus glaucus	h				NS	0.10	0.70	5.26*	NS
Eucalyptus miniata	t				NS	17.20	34.00	4.63*	NS
Galactia sp. RJF 681	h								8.30****
Rhynchosia minima	p/v								8.07****
Flemingia sp. RJF 812	p/h								7.53***
Mitrasacme connata	h/a								6.69***
Ficus opposita	t								6.48***
Planchonia careya	t								5.66***
Mitrasacme latiflora	h								5.44***
Hibiscus meraukensis	h/a								5.17***
Brachychiton diversifolius	t								4.06*
Phyllanthus sp. CRD 5596	h								4.04*
Alloteropsis semialata	g								3.50*

Species occurring in six or more quadrats that were not significantly affected by fire history, aspect or their interaction:-
Eucalyptus tetrodonta (t), E. clavigera (t), Erythrophleum chlorostachys (t), Buchanania obovata (t), Brachychiton paradoxus (t), Persoonia falcata (t), Cycas armstrongii (pa), Tinospora smilacina (v), Distichostemon hispidulus (s/s), Petalostigma quadriloculare (s/s), Coelorachis rottboellioides (g), Euphorbia vachellii (h), Knoxia stricta (h), Sauropus brunonis (h), S. dittassoides (h), Dunbaria singuliflora (p/v), Desmodium 'clavitricha' *p/h/a)*
**** P<0.001, *** P<0.01, ** P<0.02, * P<0.05, NS P>0.05. Letters denotes means not significantly different at P<0.05
t- tree, pa- palm, s/s- sub-shrub, v-vine, p- pea, g- grass, gm- graminoid, h- herb, a- annual

None of the lifeform groups seemed to particularly favour either ridge face. The species that showed significant response to the interaction of fire history and aspect are shown in Table 4.5.

Table 4.5 Mean (and s.e.m.) percentage cover of those species significantly responding to the interactive effect of fire history and aspect.

Sample size	South	North
No fire	10	10
Moderate	3	3
Annual	10	10

Alloteropsis semialata	South	North
No fire	14.50(2.60)	4.00(1.00)
Moderate	10.83(1.67)	10.83(1.67)
Annual	25.00(0.32)	24.00(4.54)

Brachychiton diversifolius	South	North
No fire	3.01(1.22)	0.25(0.25)
Moderate	0.00(0.00)	0.00(0.00)
Annual	0.01(0.01)	0.75(0.38)

Ficus opposita	South	North
No fire	4.50(1.43)	0.25(0.25)
Moderate	0.00(0.00)	2.50(2.50)
Annual	0.01(0.01)	0.00(0.00)

Flemingia sp. RJF 812	South	North
No fire	4.26(1.54)	8.75(3.40)
Moderate	27.50(10.00)	7.50(0.00)
Annual	2.75(0.07)	16.00(3.66)

Galactia sp. RJF 681	South	North
No fire	0.00(0.00)	0.00(0.00)
Moderate	0.00(0.00)	0.00(0.00)
Annual	3.76(1.07)	0.25(0.25)

Hibiscus meraukensis	South	North
No fire	0.53(0.33)	0.00(0.00)
Moderate	1.76(0.83)	0.00(0.00)
Annual	0.00(0.00)	0.00(0.00)

Mitrasacme connata	South	North
No fire	1.28(0.41)	0.26(0.25)
Moderate	2.50(0.00)	4.17(1.67)
Annual	2.02(0.32	0.00(0.00)

Mitrasacme latiflora	South	North
No fire	0.00(0.00)	0.25(0.25)
Moderate	0.00(0.00)	0.00(0.00)
Annual	0.04(0.02)	1.75(0.38)

Phyllanthus sp. CRD 5596	South	North
No fire	0.54(0.33)	0.01(0.01)
Moderate	0.03(0.03)	0.03(0.03)
Annual	1.75(0.38)	0.01(0.01)

Planchonia careya	South	North
No fire	16.00(3.66)	16.50(3.56)
Moderate	10.83(1.67)	10.83(1.67)
Annual	7.50(1.29)	27.00(4.31)

Rhynchosia minima	South	North
No fire	0.00(0.00)	0.00(0.00)
Moderate	2.50(2.50)	0.83(0.83)
Annual	3.00(0.82)	0.00(0.00)

4.3.3 Fire and aspect effects on vegetation structure

Total basal area and that of the dominant tree species *Eucalyptus tetrodonta* and *Eucalyptus miniata* and the sub-dominant *Erythrophleum chlorostachys* were not significantly affected by fire history ($P>0.1$). This would be expected if the vegetation along the ridge was homogeneous prior to fire exclusion.

Total basal area of the overstorey was not significantly influenced by aspect. The only overstorey species whose basal area was significantly affected by aspect was *Eucalyptus miniata* which was more dominant on north than south facing slopes ($P<0.05$). *Terminalia ferdinandiana* saplings were more abundant on south than north facing slopes (Table 4.6). Total sapling numbers increase progressively from annually burnt sites to fire free sites (Table 4.6). All of the woody species lifeform groups were significantly more abundant as saplings in the midstorey of the unburnt Solar Village forest (Table 4.6). Most individual woody species that were relatively abundant in the midstorey showed the same trend although *Eucalyptus miniata* and *Erythrophleum chlorostachys* seemed to be disfavoured by annual burning rather than particularly favoured by complete fire protection. *Terminalia ferdinandiana* was significantly favoured on the moderately burnt site (Table 4.6). *Eucalyptus miniata, Acacia aulacocarpa, Acacia mimula* and *Cycas armstrongii* were the only relatively common woody species that showed no response to fire history as a main affect although the former three of these species were significantly affected by the interaction of fire and aspect (Table 4.7). The latter species is long lived and slow growing.

Table 4.6 Two-way ANOVA results showing mean scores for saplings (per 100 m^2) and the significance of fire and aspect effects; and the significance of fire-aspect interactions.

	Fire history				Aspect			Fire x Aspect
Plant species	No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n=23)	F value	F value
Erythrophleum chlorostachys	2.1a	3.2a	0.1	10.08****			NS	NS
Planchonia careya	3.5	1.5a	0.9a	12.88****			NS	NS
Eucalyptus tetrodonta	1.1a	0.5ab	0.2b	6.49***			NS	NS
Buchanania obovata	1.1	0.0a	0.4a	4.47**			NS	NS
Terminalia ferdinandiana	2.4a	3.3a	1.8a	4.62**	3.4	1.1	20.18****	NS
Xanthostemon paradoxus	1.7a	1.2ab	0.1b	4.09*			NS	NS
Eucalyptus miniata								4.56**
Acacia mimula								4.65**
Acacia aulacocarpa								4.01*
Total acacias							NS	4.6*
Total broad-leaved species	11.5a	10.2a	3.3	15.75****			NS	NS
Total eucalypts	3.2a	1.8ab	0.6b	12.20****			NS	NS
Total saplings	22.5a	16.0a	5.1	29.19****			NS	NS

Relatively frequent species not significantly affected by fire, aspect or their interaction:- *Cycas armstrongii*

**** P<0.001, *** P<0.01, ** P<0.02, * P<0.05, NS P>0.05

letters denote means not significantly different at P<0.05

Table 4.7 Mean (and s.e.m.) densities of saplings (mean no. per 100 m^2) of those species significantly responding to the interactive effect of fire history and aspect.

	Eucalyptus miniata			*Acacia mimula*	
	South	North		South	North
No fire	1.0(0.3)	0.7(0.3)	No fire	0.0(0.0)	2.1(0.8)
Moderate	0.0(0.0)	2.0(1.2)	Moderate	0.0(0.0)	0.0(0.0)
Annual	0.3(0.2)	0.1(0.1)	Annual	0.3(0.3)	0.2(0.1)
	Acacia aulacocarpa			Total acacias	
	South	North		South	North
No fire	0.5(0.2)	5.7(2.2)	No fire	1.0(0.3)	8.1(2.4)
Moderate	0.0(0.0)	0.0(0.0)	Moderate	0.0(0.0)	0.0(0.0)
Annual	0.2(0.2)	0.1(0.1)	Annual	0.5(0.3)	0.3(0.2)

4.3.4 Fire effects on woody sprout density

ANOVA revealed five tree species disproportionately distributed according to fire history and aspect that were present in the ground layer as woody sprouts (Table 4.8 and 4.9). Lignotuberous *Planchonia careya* is more frequent in areas burnt by annual fires. The greater abundance of *Terminalia ferdinandiana* saplings on the southwestern slope is reflected by the distribution of lignotuberous individuals of this species.

4.4 Discussion

In temperate Australian eucalypt forests cohorts of tree seedlings germinate after fire (Ashton 1981, Christensen *et al.* 1981, Wellington and Noble 1985). This model seems unsuitable in the eucalypt forest of the monsoon tropics where fires are frequent and tree seedlings rarely observed. At the Solar Village there was no consistent response to fire frequency from the ten common tree species in the ground layer. Six species were not significantly affected by fire. The response of three species seems dependent on site factors and *Planchonia careya* was more abundant with frequent firing. The enigma of tree establishment in these forests warrants further attention.

Table 4.8 Two-way ANOVA results showing mean scores for lignotuberous resprouts (per 100 m^2) and the significance of fire and aspect effects; and the significance of fire-aspect interactions.

	Fire history				Aspect			Fire x Aspect
Plant species	No fire (n=20)	Moderate burning (n=6)	Annual burning (n=20)	F value	South (n=23)	North (n=23)	F value	F value
Planchonia careya	6.4a	5.6ab	12.0b	4.95**			NS	NS
Terminalia ferdinandiana				NS	8.2	2.0	15.60****	NS
Acacia aulacocarpa								7.89****
Erythrophleum chlorostachys								5.85***
Xanthostemon paradoxus								4.73**
Total lignotugerous regrowth	76.0ab	109.0ab	58.0b	4.61**	30.5	21.2	4.61**	NS

Relatively frequent species not significnatly affected by fire, aspect or their interaction are:
Acacia mimula, Buchanania obovata, Terminalia ferdinandiana, Eucalyptus miniata, Eucalyptus tetrodonta;
also total broadleaved shrubs, eucalypts and acacias.

**** P<0.001, *** P<0.01, ** P<0.02*, P<0.05, NS > 0.05
letters denote means not significantly different at P<0.05

Table 4.9 Mean (and s.e.m.) densities of woody sprouts (mean no. per 100 m^2) of those species significantly responding to the interactive effect of fire history and aspect.

	Acacia aulacocarpa			*Erythrophleum chlorostachys*	
	South	North		South	North
No fire	1.7(1.6)	10.9(3.1)	No fire	8.7(2.1)	4.8(1.9)
Moderate	0.8(0.8)	0.0(0.0)	Moderate	3.6(1.8)	20.9(4.9)
Annual	1.1(1.1)	1.1(0.7)	Annual	3.1(1.0)	2.5(0.8)

	Xanthostemon paradoxus	
	South	North
No fire	8.7(3.2)	2.0(1.2)
Moderate	0.8(0.9)	12.0(10.1)
Annual	0.0(0.0)	0.3(0.3)

The Munmalary forest site and the Solar Village are dominated by the same eucalypt species yet despite broad similarities between these sites differences are evident. The accession of dominant eucalypt species from ground layer to saplings and the formation of a broadleaved midstorey at the Solar Village but not at Munmalary is statistically clear. The difference in vegetation response to fire between the sites is further reflected by comparison of individual species. Saplings of the tree, *Erythrophleum chlorostachys* developed in the absence of fire at both sites. However, this was the only one of 22 relatively frequent species that occur at the Solar Village or in either Munmalary's forest or woodland that showed preference to similar fire histories (D. M. J. S. Bowman and B. A. Wilson unpublished data).

The differences between responses at the Solar Village and Munmalary lead to the conclusion that the interplay of edaphic conditions with types of fire frequency elicits different responses from individual species. Furthermore, apparently subtle site differences alter the response of some species to fire in ways that are greater than the separate influence of the intrinsic site factor or the imposed fire condition.

Bowman (1988) provided a mechanistic model suggesting that broadleaved trees gain access to the forest mid-canopy where

favourable moisture conditions extend the growing season and there is some relief from fire. This combination of factors allows these species to attain a size resistant to the damaging effect of fire.

This model was based largely on the Munmalary evidence where the development of broadleaved midstoreys following fire protection was more likely to occur in woodland occupying a range of sites but dominated by different *Eucalyptus* species from those that dominate the forests (Bowman 1988a). However, the suggestion that structural changes occur on these sites because conditions are more favourable is not supported by the evidence from Melville Island where an examination of soils, seasonal moisture cycles and root profiles in open eucalypt vegetation suggests that forests occupy the best sites (Chapter 2). Furthermore, the soil moisture conditions on the rocky Solar Village ridge are probably more severe than for the deep red earths supporting forest at Munmalary. Nevertheless shifts in structure and abundance of overstorey species as a result of variations in fire conditions do seem more probable on particular sites. Rockiness may be one such factor that effects the mutability of Top End vegetation. Bowman *et al.* (1990) have invoked the interplay of past fire conditions and site variation to account for a woodland complex that is heterogeneous without apparent environmental correlation on the widespread metamorphic rocks in the Pine Creek-Katherine area. This suggestion is supported by the greater response of forest vegetation to fire exclusion on the rocky soils of the Solar Village ridge compared to similar forests on the deep soils at Munmalary. The existing evidence seems to indicate that changes in structure and overstorey composition for tropical eucalypt vegetation is more probable where the physical conditions of a site impose stress.

CHAPTER 5 STAND STRUCTURE AND COMPETITIVE INFLUENCES ON REGENERATION IN THE TROPICAL EUCALYPT FOREST

5.1 Introduction

Stand structure is frequently used to interpret the regeneration process of forests. If the arrangement of stem size classes has a reverse J-shape with many small stems and gradually declining numbers of larger stem sizes regeneration is interpreted as being continuous (Hett and Loucks 1976). Stand structures that deviate from this model generally reveal a peak in abundance of one or more size classes that represent a cohort of individuals from previous regeneration events. The regeneration event is usually precipitated by intermittent broadscale disturbance phenomena (eg. Withers and Ashton 1977, Veblen and Ashton 1978).

Braithwaite and Estbergs (1985), Werner (1986) and Wilson and Bowman (1987) have emphasized the lack of sapling and pole sized trees in most tropical eucalypt forest. This fact has lead some authors to suggest that conditions that previously favoured forest regeneration no longer prevail and that current conditions are not suitable for the maintenance of forest structure. It has been suggested that the current fire regime (Bell 1981, Braithwaite and Estbergs 1985) possibly in combination with the arrival of large herbivores such as the Asian water buffalo (*Bubalus bubalis*) (Werner 1986) may inhibit the regeneration process, resulting in depletion of the overstorey.

Chapter 3 established that the growth of woody sprouts is limited regardless of fire. Evidence from fire protected forest at Munmalary documented that overstorey species and the frequent broadleaved understorey trees did not develop as midstorey in the absence of fire (Bowman *et al.* 1988a). Only short lived *Acacia* spp. and *Erythrophleum chlorostachys* developed as saplings following fire protection at Munmalary. However, in the fire protected woodland at Munmalary and the forest on the rocky ridge described in Chapter 4, mixed species midstoreys developed. Wilson and Bowman (1987) describe forest near Darwin that was felled by Cyclone Tracey. The

prominent sapling layer in this forest suggests that overstorey may suppress the regeneration of woody sprouts, while the influence of site and fire conditions on this process remains uncertain.

It is well recognised that the influence of overstorey trees inhibits regeneration in some temperate Australian biomes. In many eucalypt forests relief from overstorey competition determines the release of suppressed lignotuberous regrowth (Abbott and Loneragan 1984, Bowman and Kirkpatrick 1986a, Incoll 1979).

The tropical eucalypt forest and woodland of northern Australia are savanna by definition because of the coexistence of trees and grass. The competitive influence of trees on grass in savanna ecosystems is well recognised by range land managers. Walker *et al.*'s (1972) evidence that herbage increases three-fold with the removal of trees provides the economic rationale for the proposed destruction of the poplar box (*Eucalyptus populnea*) overstoreys in central Queensland. Examination of the reverse relationship, the inhibition of woody growth by understorey, has received less attention. Knoop and Walker's (1985) work from southern Africa indicates that tree growth in *Acacia* woodland was inhibited by competition from herbage although this interaction was not evident in a broadleaved woodland. If overstorey competition is occurring in the tropical eucalypt forest, our understanding of the regeneration process will not be complete until the mechanism of suppression is determined.

This study presents the stand structure of tree species in a typical Melville Island savanna forest and continues with studies designed to examine the influence of competitive interactions on tree regeneration within these forests. The central experiment described in this chapter investigates the hypotheses that: 1) overstorey trees inhibit the regeneration of woody sprouts; 2) grass inhibits the regeneration of woody sprouts; 3) *Acacia* regrowth inhibits the regeneration of woody sprouts. The latter hypothesis is suggested in the light of the fire protected forest at Munmalary where *Acacia* regrowth was frequent but regrowth of nearly all other tree species was infrequent. The first hypothesis is further explored by

investigation of the spatial distribution of saplings in undisturbed forest and documentation of some abandoned forestry experiments.

Abbott and Loneragan (1984) have demonstrated that jarrah (*Eucalyptus marginata*) have little chance of success unless there lignotubers are at least 15 cm long. Lignotuber size may be a reflection root carbohydrate reserves. Miyanishi and Kellman (1986) have demonstrated that severing of shoots by fire dramatically depletes root starch reserves in some tropical savanna shrubs. Furthermore, the decline of root starch following severence of aboveground parts has been demonstrated for other tree species (Woods *et al.* 1959, Willard and McKell 1973). It has also been shown that death (Miyanishi and Kellman 1986) and the cessation of growth (Tew 1970) for woody stems can be related to root carbohydrate reserves. Regeneration in the tropical eucalypt forest is lignotuberous and Chapter 3 showed that under the intact forest with 1 year's protection from fire, low frequencies of individuals switch from suppressed woody sprouts condition to saplings. In light of this fact and previous research from other continents, the lignotubers of woody plants were examined in an attempt to decipher the morphological features of the lignotuber associated with stems that have switched from suppressed stem to sapling.

5.2 Methods

5.2.1 Stand structure

Stand structure data was collected from a relatively uniform area of open forest near Paru on Melville Island. *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Erythrophleum chlorostachys, Acacia aulacocarpa, Eucalyptus confertiflora, Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta* were chosen for assessment because they are common and represent a cross-section of the tree lifeforms found in the savanna forest.

Individuals in the <2 m H size class were counted in a square quadrat of 0.25 ha (Section 7.2.3); saplings (>2 m H and less than <10 cm dbh) in a 20 m wide transect totalling 3.8 ha (Section 5.2.2); and trees >10 cm

in a portion of the same 20 m wide transect totalling 1.6 ha (Section 5.2.2).

5.2.2 Association of saplings in natural canopy gaps

A long transect line was established through an area of open eucalypt forest. Whenever a sapling of any species (>2 m tall and < 10 cm dbh) occurred within 10 m either side of the transect line, its position on the transect was noted. If the sapling was one of five target species (*Eucalyptus miniata, Eucalyptus tetrodonta, Erythrophleum chlorostachys, Terminalia ferdinandiana* and *Acacia aulacocarpa*) the distance from the sapling to neighbouring trees within a 10 m radius was noted. The dbh and minimum and maximum radius of the crown of the neighbouring trees was recorded. The transect was continued along a compass bearing until at least 50 of the target species were located. Only 42 *Eucalyptus miniata* saplings were located after 1900 m of transect. In order to determine a comparative measure of competition around random points the same information was collected from 52 coordinates spaced every 20 m on the transect.

The competition index (CI) of Ellis *et al.* (1987) was used to give a single expression of competitive influence of overstorey trees surrounding a sapling. The formula is as follows:

$$CI = \sum_i \frac{(d_i/x)}{1+\exp(-10.5+0.75(D_i/d_i)}$$

where:

d_i = the diameter of the ith competitor

D_i = the distance to the ith competitor

x = diameter of the subject sapling

Frequency histograms of CI were prepared for each species and a histogram of CI for random points (CIr) was calculated for each species. For determining CIr for a species, the assumption was made that x has the same range of values as for the saplings of that species. The histograms of CI and CIr were compared for each species using the chi-squared test and the values of these indices compared using the Mann-Whitney U-test.

5.2.3 Competition experiment

Four plots were established in an apparently uniform area of open eucalypt forest. The sites were burnt during July 1986. At least 20 individuals in each plot of *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus tetrodonta, Eucalyptus miniata, Eucalyptus confertiflora* and *Acacia aulacocarpa* were located, tagged, mapped and measured in the same way as has been described in Section 3.2.1. The plots were of sufficient size to encompass the required number of each species and therefore had variable area. The following treatments were applied to the plots.

a) A control with no treatment (area: 860 m^2).

b) Overstorey and most untagged lignotuberous eucalypts killed (area: 860 m^2).

c) *Acacia* trees removed (area: 1240 m^2).

d) Herbage removed (area: 700 m^2).

Overstorey was killed by injection of the tree herbicide Tordon®. Trees around the perimeter of the plot were also killed if their crowns reached the plot boundary. Thirty-three trees with a total basal area of 1.15 m^2 were killed. Most untagged lignotuberous individuals were killed by painting Tordon® onto severed regrowth butts. *Acacia* individuals were removed with a mattock. Herbage was removed by hand weeding around each tagged woody sprout within a 0.75 m radius. The last two treatments required ongoing maintenance. All plots were fire protected during the 1987 dry season by burning around the perimeter of the site on a calm evening. The species and dbh of the overstorey was noted. All stems of the tagged individuals were measured at the end of the dry season (15-17/11/87) and after the following wet season (4-6/4/88). Untagged 'breakaway' saplings (either >2 m H or >1 cm diameter at the base) were tagged, measured and mapped. No fire protection was attempted after 1987 and the sites were burnt in the dry season of 1988 and 1989. Saplings that survived these fires were counted on 6/12/89.

A pressure bomb was used to determine leaf xylem pressure potentials in the tree killed plot and control. Measurements were performed

using new leaves of *Eucalyptus confertiflora* and *Buchanania obovata* and old leaves of *Eucalyptus tetrodonta* (n>8 in all cases) on 1/10/87.

Five soil sample replicates were obtained from 15, 45, 90 and 150 cm depths in the tree killed and control plots on the 20/8/87 and sealed in jars.

The height and number of stems of each individual were divided by their initial values and then compared between treatments using the Kruskal-Wallis test. The data were further analysed by comparing each treatment to the control using the Mann-Whitney U-test.

Gravimetric soil moisture content was determined by weighing the samples before and after drying at 105° C for 24 hours. Xylem pressure potential and gravimetric soil moisture values were compared between treatments using the Mann-Whitney U-test.

5.2.4 Old experimental sites without overstorey

There are several old experimental sites in open forest on Melville Island where the overstorey has been removed. Site history records are available for three of these plots. The author prepared one site and written records for two more plots were kindly provided by M. Haines (Conservation Commission of the Northern Territory)

1) The overstorey on two small plots (1000 m^2 each) near Yapilika was killed using the tree poison Tordon® on 8/11/86. The plots escaped fire in 1987 but were burnt during the dry season of 1988. In each of these plots, two 20 x 20 m sub-plots were located so that no live tree crowns covered their area.

2) A field trial was commenced on the road between Yapilika and Pularumpi by the Forestry Service in 1973. At this site the overstorey was clearfelled from a 1 ha plot. The species and dbh of the clearfelled trees were available from the original records. The experiment was abandoned soon after establishment and the plot has had a history of regular burning since this time. The plot is 100 x 100 m and a 20 m buffer was excluded from measurement leaving space for nine contiguous 20 x 20 m sub-plots.

3) In 1972 CSIRO established a comprehensive experiment on Karslake Peninsula designed to examine the effects of clearing and burning on regeneration. The clearfelled area was about 60 ha. It was fire protected for at least 10 years after establishment but has been regularly burnt since 1985. The control plot has an intact overstorey and has been burnt regularly since the early abandonment of the experiment. Ten 20 x 20 m sub-plots were spaced at 10 m intervals in the clearfelled block. These plots were parallel to and 20 m distant from the control-clearfelled boundary track. Matching sub-plots were placed in the control plot.

The 20 x 20 m sub-plots at these three sites were measured during November 1988. In each sub-plot the species and dbh of all live stems greater then 2 m H were noted. In a 1 m strip around the perimeter of each sub-plot the species and number of trees less than 2 m H were recorded.

The Yapilika and Pularumpi Road clearfelled blocks abut intact forest. Two 45 m transects were placed across the boundary at these sites. Saplings were counted in 20 x 5 m quadrats whose long axes were parallel to the boundary.

Size class histograms of regeneration in the tree killed plots were prepared. Size and frequency of regeneration between the Karslake and Pularumpi Road blocks were compared using the Mann-Whitney U-test.

5.2.5 Investigations of the lignotuber

The Yapilika tree killed block were chosen as the first site for excavation of lignotubers because there were obvious patches of sapling *Eucalyptus nesophila* regeneration alongside stunted lignotuberous stems. Lignotubers of 17 breakaway saplings (>2 m H or >1 cm at the base) and 15 short regrowth stems were excavated and sketched in the field. The lignotubers were described by noting the dimensions of the smallest rectangle that could enclose their area (lignotuber area index, Fig. 5.6), the heights and numbers of active shoots, the presence and diameter of tap and lateral roots and the

extent of decay (presence of hollows or a fragmented circumference). *Eucalyptus tetrodonta* saplings at this site were excavated and described in the same manner.

A total of 180 lignotubers of *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Eucalyptus miniata* and *Eucalyptus confertiflora* from a forest near Milikapiti were examined using the method described above. Part of this sample deliberately included sapling size stems of each species. These data were supplemented by a non-destructive sampling technique where stems were measured and lignotuber size was assessed using a metal probe.

The relationship between lignotuber size and stem height was illustrated graphically and explored using Pearson's product moment correlation coefficient. Deviations in the distribution of lignotuber size classes between stunted lignotuberous stems and saplings were tested using the chi-squared test. The relationship between stem height and the following lignotuberous features were explored for each individual species using the Mann-Whitney U-test:
1) tap root vs no tap root; 2) intact tap root vs others; 3) large tap root (greater than the 25% quartile for the lignotuber area index) vs others; 4) large intact tap root vs others.

5.3 Results

5.3.1 Stand structure

Size class histograms for nine open forest tree species are presented in Fig. 5.1. It is evident that *Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta* dominate the tree size classes. The only other species that occasionally joins these trees in the canopy is *Erythrophleum chlorostachys*. The stand structures of *Buchanania obovata* and *Planchonia careya* are unusual in that they are entirely represented by short woody sprouts. Saplings are present for all other species although there is an extreme disparity between stems less than 2 m high and saplings. The disparity between these size classes is most evident for *Erythrophleum chlorostachys* and least evident for *Terminalia ferdinandiana*. There is an even distribution of trees

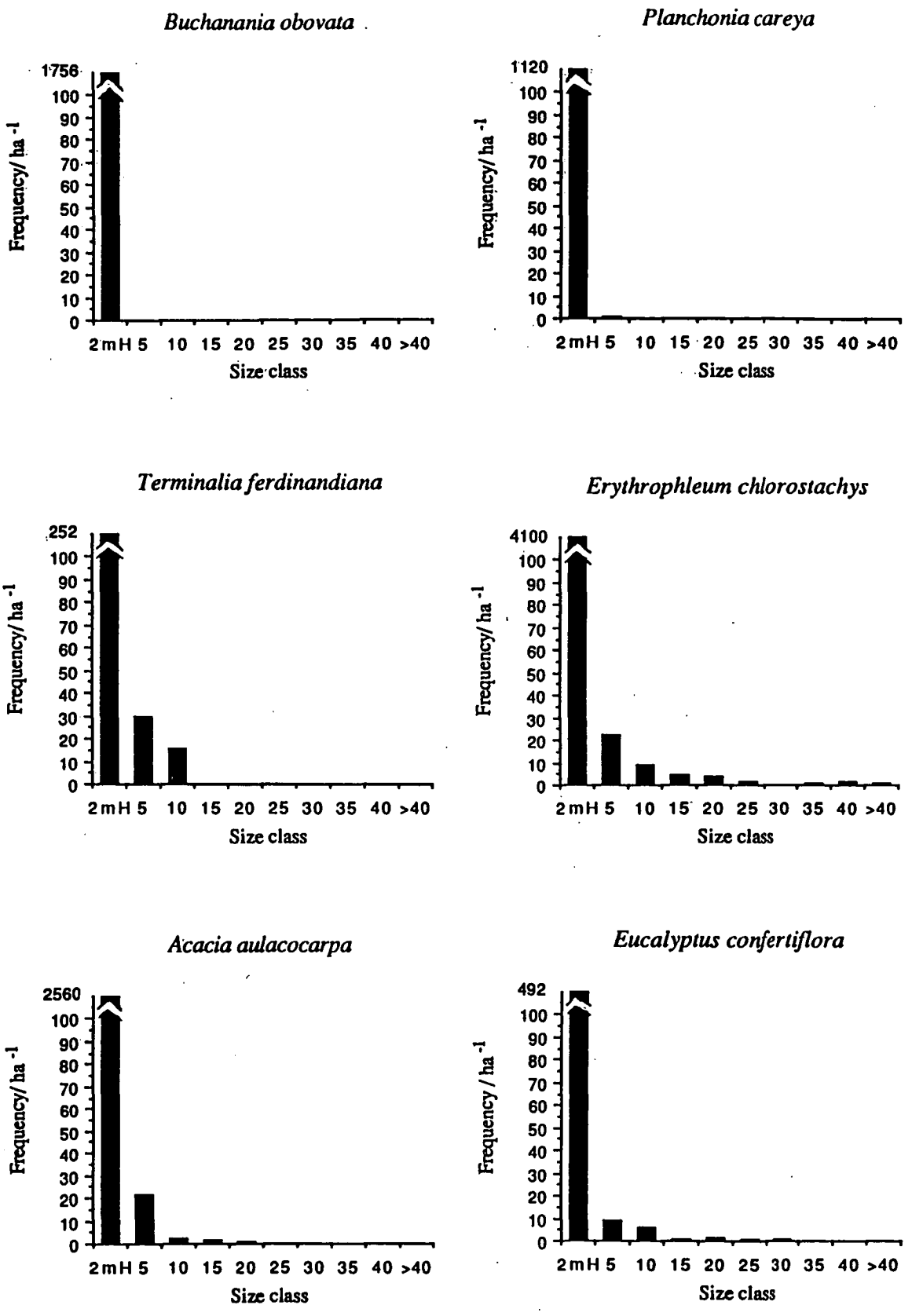


Figure 5.1 Size class histograms of nine open forest tree species near Paru, Melville Island. Stem size classes are indicated by the maximum dbh for each class.

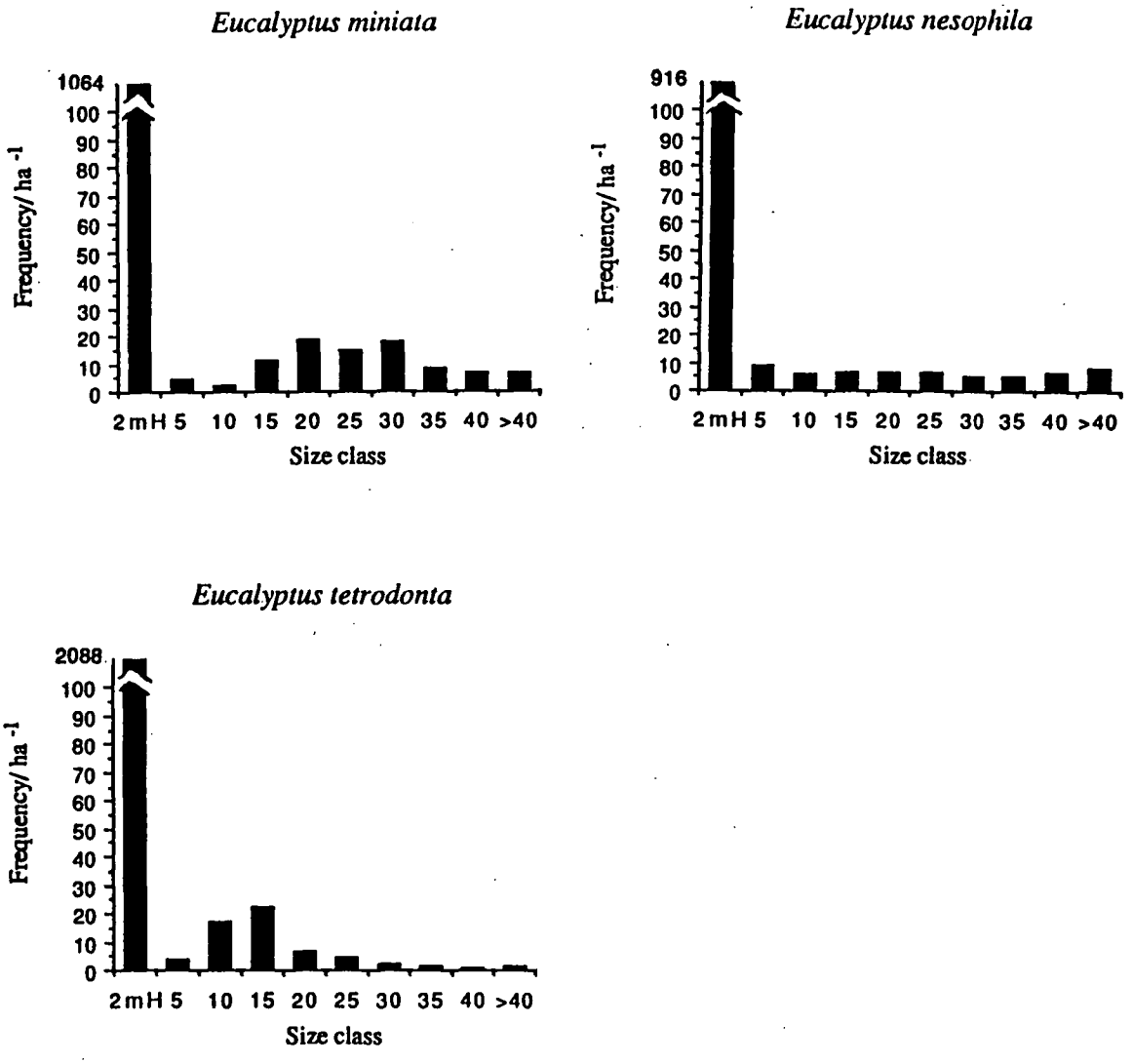


Figure 5.1 continued

across the size classes taller than 2 m for the dominant overstorey tree *Eucalyptus nesophila*. *Eucalyptus miniata* has very low densities of saplings but is well represented by larger trees. The population structure of *Eucalyptus tetrodonta* indicates a peak in the abundance of trees in the size class between 5 and 15 cm dbh.

5.3.2 Association of saplings in natural canopy gaps

If saplings were strongly influenced by overstorey competition, frequency distributions that are strongly skewed toward low CI classes relative to the distribution of CIr would be expected. The chi-squared test revealed that the discrepancy between observed and random was significant for *Terminalia ferdinandiana* ($P<0.05$), *Erythrophleum chlorostachys* ($P<0.01$) and *Eucalyptus miniata* ($P<0.01$) (Fig. 5.2).

Observed CI were significantly lower than random for the latter two species (Mann-Whitney U-test; $P<0.01$ and $P<0.02$ respectively). *Terminalia ferdinandiana* does not seem to be associated with areas of lower overstorey competition (Fig. 5.2) and there was no statistically significant variation from random for *Eucalyptus tetrodonta* or *Acacia aulacocarpa* saplings. Substantial regeneration is also occurring where CI is moderate despite the occurrence of sapling *Erythrophleum chlorostachys* and *Eucalyptus miniata* in significantly greater proportion where CI is lower (Fig. 5.2).

5.3.3 Competition experiment

There were virtually no significant differences between height and number of stems for any species at both measuring times between the treatments of the competition experiment. No comparisons were significant at the $P<0.01$ level for the 32 tests across treatment groups (length and number of stems for eight species at two measuring times) or the 96 individual comparisons between the treatment and control plots. The few tests that were weakly significant ($P<0.05$) almost certainly represent alpha error as there was no consistency in the nature of the result. Table 5.1 shows the distribution of breakaway saplings following 2 years of treatment and after the dry season fires of 1988 and 1989. While individual numbers were low, there are some

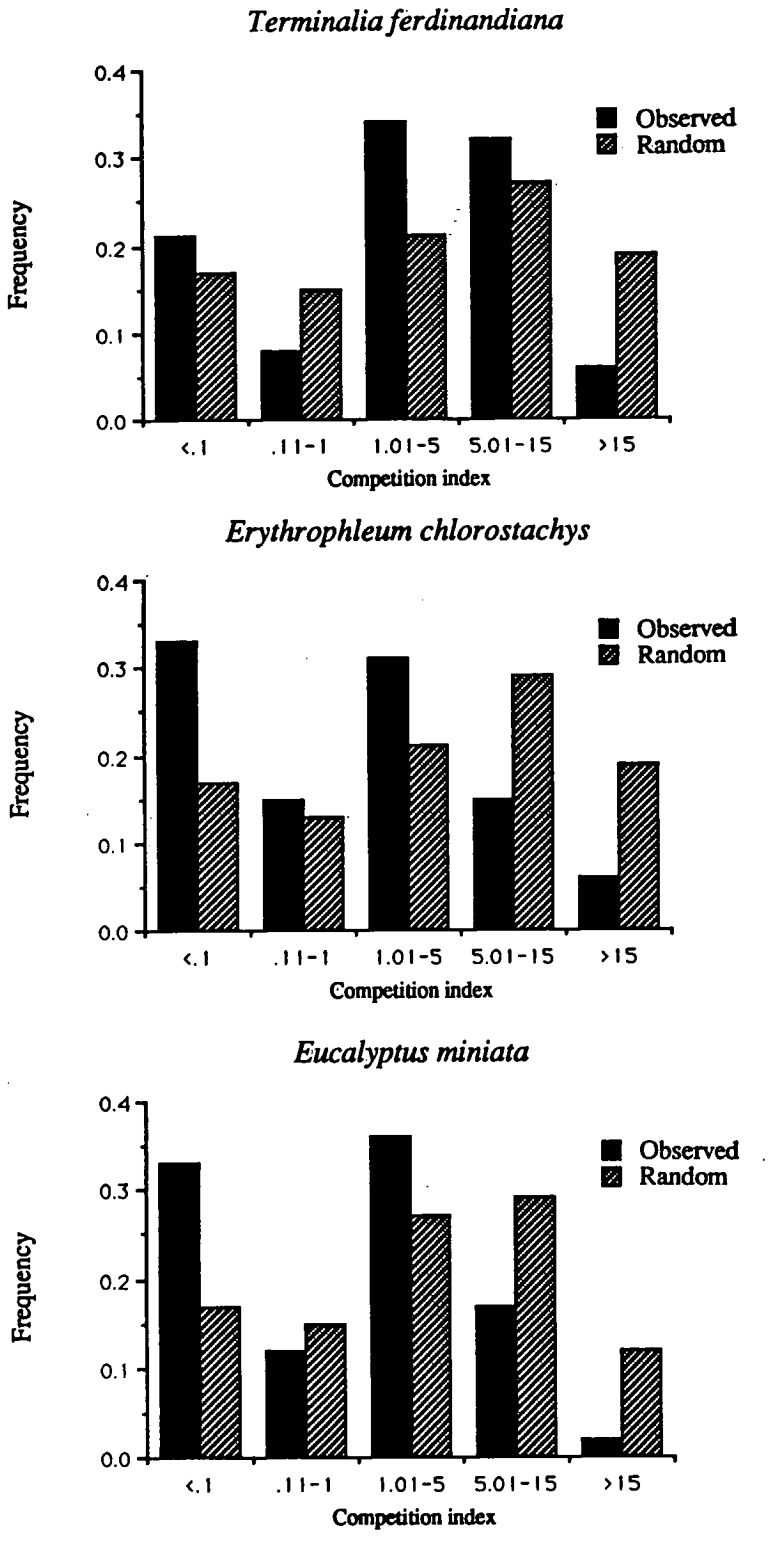


Figure 5.2 Histograms of competition index values for the observed sapling distribution (CI) and the competition index values if saplings occurred randomly. Only species with significant differences ($P<0.05$), as determined by the chi-squared test, between observed and random competition values are shown.

Table 5.1 Densities of breakaway saplings (stems ha^{-1}) according to experimental treatment. The 'no grass' treatment is not included because the treatment did not affect the whole treatment block as it was only applied around the tagged plants.

	Control		Tree killed		Acacia killed	
Species	before fire	after fire	before fire	after fire	before fire	after fire
Eucalyptus miniata	92.8	0.0	34.8	11.6	80.8	10.2
Other eucalypts	23.2	0.0	0.0	11.6	24.2	10.2
Grevillea decurrens	23.2	0.0	127.5	0.0	16.2	8.1
Acacia spp.	440.6	46.4	915.9	0.0	removed	removed
Erythrophleum chlorostachys	11.6	23.2	58.0	23.2	8.1	0.0
Broad leaved species	58.0	11.6	150.7	0.0	16.2	0.0
Total saplings	649.3	81.2	1287.0	46.4	145.5	28.5
Plot area (sq. m)	860		860		1240	

indications that eucalypts have a greater chance of reaching sizes that avoid the damaging effect of fire after release from overstorey competition. The only plots with breakaway eucalypts were the tree killed and *Acacia* killed plots (Table 5.1). The proportion of breakaway *Eucalyptus miniata* saplings is greater in the tree killed plot than other treatments. This is because all but 20 tagged lignotuberous individuals were killed. There were many more than 20 *Eucalyptus miniata* individuals at other sites. The successful sapling in the tree killed plot grew from 1 to 5 m H during 12 months in the tree killed plot (Fig. 5.3). The most rapid growth occurred during the second wet season and the sapling had reached sufficient height to survive the fires of two subsequent dry seasons.

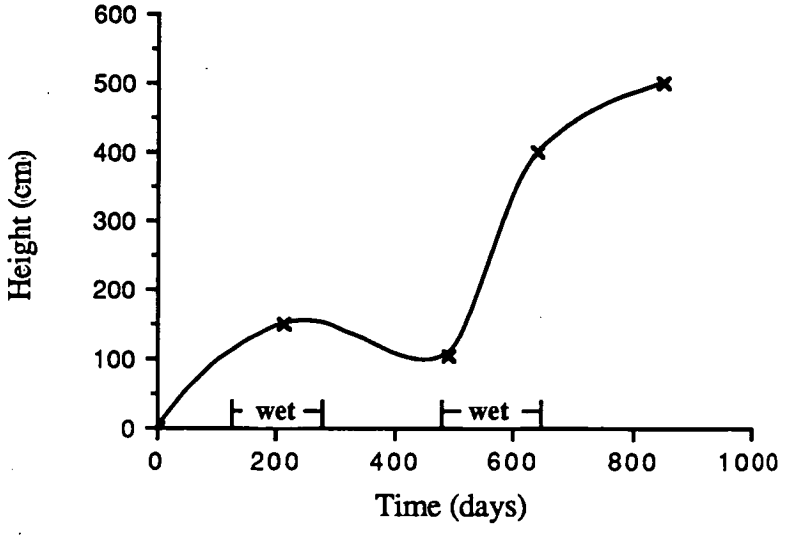


Figure 5.3 Growth of a single breakaway *Eucalyptus miniata* sapling in the tree killed plot of the competition experiment.

Soils were significantly moister on the tree killed block at 150 cm ($P<0.05$, n=5) although this relationship was insignificant at shallower depths ($P>0.05$). Xylem pressure potential of the measured plant species was not significantly different between the tree killed and control treatments ($P>0.05$ in all cases).

5.3.4 Old experimental sites without overstorey

One of the tree killed blocks (80 m^2) at Yapilika had virtually no saplings (Table 5.2). Less than 30 m away in the second tree killed block there were 19 *Eucalyptus nesophila* saplings in one sub-plot and 16 in the neighbouring sub-plot (Table 5.2). This discrepancy cannot be accounted for by the lack of potential trees in the ground layer as the densities of woody sprouts in the two blocks is similar (Table 5.2). Lignotuberous and rhizomatous individuals of *Eucalyptus tetrodonta* were plentiful in both blocks although there were virtually no saplings (Table 5.2).

Prior to clearing the total basal area of the Karslake and Pularumpi Road sites was similar (9.3 vs 10.2 $m^2 . ha^{-1}$ respectively) although the density of stems was 107 ha^{-1} at Pularumpi Road and 165 ha^{-1} at Karslake. Size class histograms of regrowth at the Pularumpi Road and Karslake Peninsula clearfelled blocks are depicted in Fig. 5.4. It is

---

Table 5.2 Original basal area ($cm^2 .20 m^{-2}$), sapling and woody sprout densities (20 m^{-2}) for two year old tree killed plots at Yapilika.

	Eucalyptus tetrodonta			*Eucalyptus nesophila*		
	Original overstorey basal area	Woody sprouts	Saplings	Original overstorey basal area	Woody sprouts	Saplings
Block 1						
Sub-plot1	1031	92	0	796	66.3	19
Sub-plot 2	707	194	0	616	143	16
Block 2						
Sub-plot 3	142	281	1	1233	107	0
Sub-plot 4	430	153	0	0	51	1

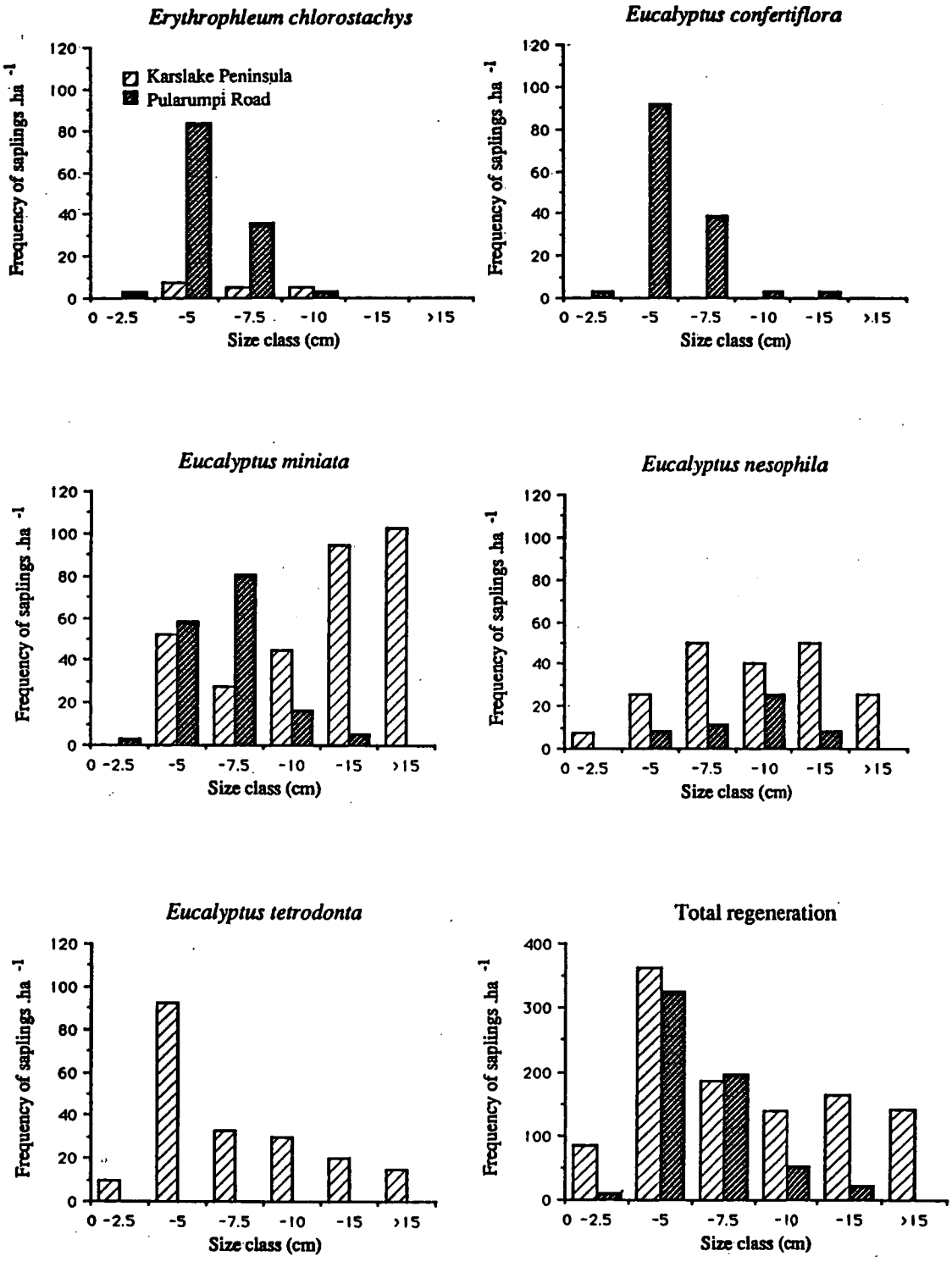


Figure 5.4 Frequency size class histograms of sapling regeneration at the Karslake Peninsula and Pularumpi Road clearfelled blocks.

clear from this figure that regeneration was far more advanced at Karslake than at Pularumpi Road. This is verified statistically as both density and size of regrowth is statistically greater in terms of the dominant eucalypts and other species combined ($P<0.001$). There were significantly more saplings of *Erythrophleum chlorostachys* and *Eucalyptus confertiflora* ($P<0.001$ in both cases) at the Pularumpi Road block than at Karslake although this may partly be a result of greater original densities of woody sprouts at the former site ($P<0.001$ in both cases). However, inspection of the surrounding bush and original records of the sites reveals that *Erythrophleum chlorostachys* is much more common in the overstorey at Karslake than at the Pularumpi Road site.

Fig. 5.5 shows the relationship between the abundance of regenerating stems and the distance from the forest canopy at Pularumpi Road and Yapilika. There is a steady increase in saplings with distance from the forest at Pularumpi Road. This relationship is less evident but still clear at Yapilika. Sapling densities decrease within the forest up to 20 m from the forest-clearing boundary and increase 25 m from the boundary within the clearing. These facts suggest that the influence of overstorey root systems extends a considerable distance from mother stems.

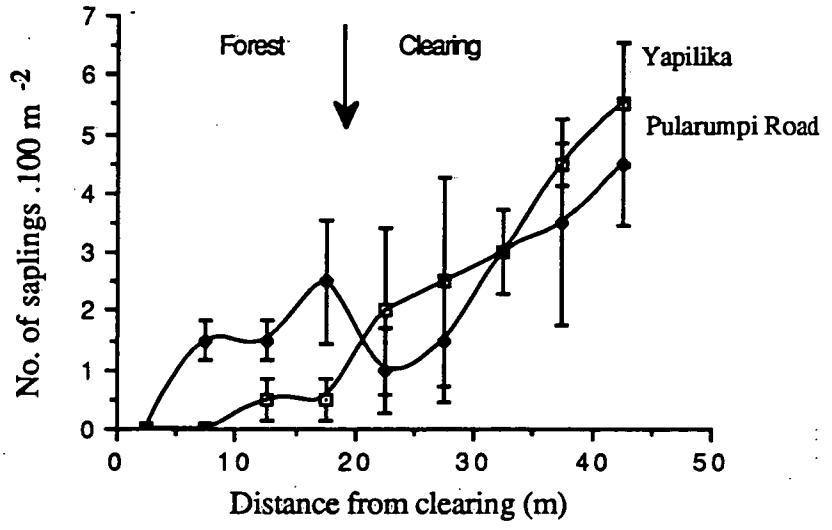


Figure 5.5 Sapling densities with increasing distance from the center of the clearing at Pularumpi Road and Yapilika. Standard error of the mean is indicated.

5.3.5 Investigations of the lignotuber

It was evident that there is considerable variation in the size and shape of lignotubers for each species. Nevertheless, there are some features that are common for particular species. *Planchonia careya* often has large lignotubers with many active buds. Decomposition of the centre of the organ and growth and expansion at the extremities results in the lignotubers of this species having a 'fairy ring' form (Plate 5.1). The lignotuber of other tree species such as *Eucalyptus nesophila* are also convoluted in shape and frequently large in size (Plate 5.2). *Eucalyptus miniata, Eucalyptus confertiflora, Buchanania obovata* and *Terminalia ferdinandiana* generally have smaller lignotubers than the other common tree species.

There were positive correlations between lignotuber size and the number of stems for all of the measured species ($P<0.001$). Fig. 5.6

Plate 5.1 Lignotuber of *Planchonia careya*. The centre of the lignotuber has decomposed, leaving a convoluted ring of woody tissue with many active buds.

Plate 5.2 Lignotuber of *Eucalyptus nesophila*. A sapling is attached to the right hand lobe of the organ.

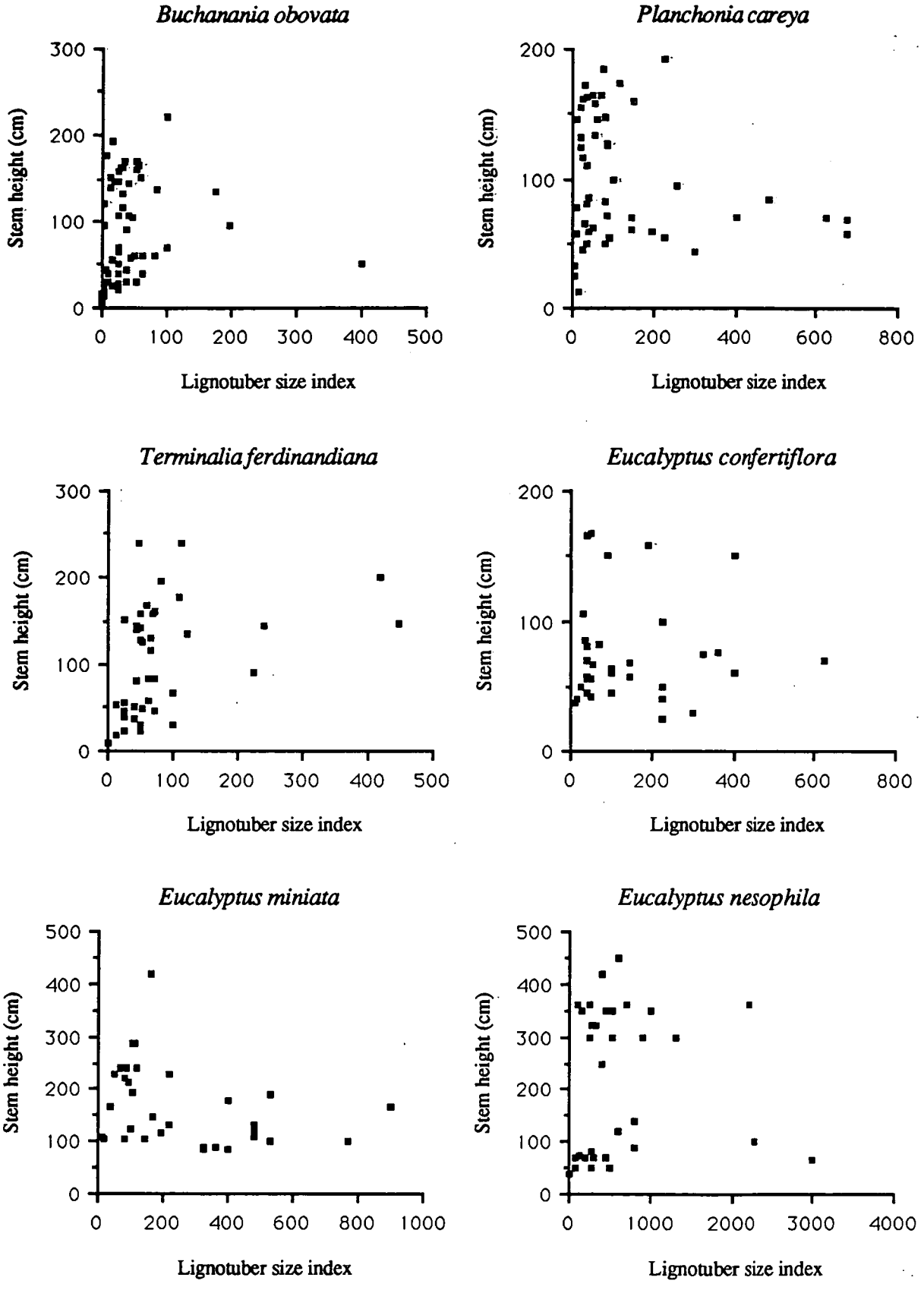


Figure 5.6 The relationship between lignotuber size and stem height for lignotuberous plants of six open forest tree species.

shows the relationship between lignotuber size and stem height. The correlation between these variables was significant for *Buchanania obovata* and *Terminalia ferdinandiana* ($P<0.05$) and not significant for the other species ($P>0.05$). Non-significant correlations may result from a declining likelihood of sapling success as lignotubers become excessively large (Fig. 5.6). The indication that sapling success is associated with middle-sized lignotubers could not be statistically verified because of the small number of individuals in the cells of a sapling size class x lignotuber size class contingency table. Nevertheless, Fig. 5.6 indicates that saplings were not found on small nor on excessively large lignotubers.

Comparisons of stem heights by various combinations of tap root features are presented in Table 5.3. Taller stems are associated with the presence of a tap root for *Buchanania obovata* and *Eucalyptus miniata*. Tall stems are associated with relatively large tap roots for *Terminalia ferdinandiana*. There was no significant relationship between stem height and the measured features of lignotubers for *Planchonia careya, Eucalyptus confertiflora* and *Eucalyptus nesophila*. Plate 5.3 shows a *Eucalyptus nesophila* sapling attached to a lignotuber without a tap root.

Table 5.3 Mean stem height according to various groupings of lignotuber features.

Species	Tap root vs others	Intact tap root vs others	Large tap root vs others	Large intact tap root vs others
Buchanania obovata	138.7/61.1***	138.7/61.1***	150.3/88.7***	105.0/88.7***
Planchonia careya	NS	NS	NS	NS
Terminalia ferdinandiana	NS	NS	141.2/91.0**	141.2/91.0**
Eucalyptus miniata	220.5/124.0*	227.8/122.5**	NS	NS
Ecualyptus confertiflora	NS	NS	NS	NS
Eucalyptus nesophila	NS	NS	NS	NS

* $P<0.05$, ** $P<0.02$, *** $P<0.01$, NS $P>0.05$

Plate 5.3 *Eucalyptus nesophila* sapling attached to a lignotuber without apparent tap root. The position of a former tap root is evident from the hole on the bottom of the lignotuber.

5.4 Discussion

5.4.1 Competitive influences

Many authors contend that an important functional feature of tropical savanna is the partitioning of resources between the grassy layer and the tree component (Walter 1971, Walker and Noy-Meir 1982, Goldstein and Sarmiento 1987). It is suggested that in these environments the root systems of grasses are concentrated in the surface soil layers while trees are able to exploit deeper zones. There is some evidence from this study to support this proposition. There was no growth response of the ground layer woody species following the removal of herbage. Furthermore, the fact that overstorey removal resulted in greater soil moisture at depth during the dry season suggests that trees exploit this zone. This effect was not evident at less than 90 cm depth. This result probably reflects the confinement of the root systems of ground layer plants to surface zones. Moisture reserves in surface soils are often beyond wilting point during the dry season (Section 2.3.3). During the months when moisture in the surface soil is limited woody plants can remain active because of their access to deep soil horizons.

Chapter 3 suggests that some secondary species such as the broadleaved trees may be suppressed by the tall evergreen eucalypts of the forest. There was no evidence from the competition experiment of this interaction. Very few secondary forest species had produced successful saplings after 3 years without overstorey trees (Table 5.2). This negative result may indicate that the spatial or temporal dimensions of the experiment were insufficient. McDonald (1976) has noted that *Pinus ponderosa* saplings took 4 years to respond to overstorey removal. The competitive relations between eucalypts and other tree species in the tropical eucalypt forest may not be understood until large-scale, longterm experiments are in place.

Eucalyptus tetrodonta saplings had a clumped distribution in a forest studied by Bowman (1986). He concluded that their release was controlled by overwood. However, it is clear from this study that overstorey competition provides only a partial explanation for the

suppression of tree regeneration in tropical eucalypt forest. Firstly, the saplings of three of five measured tree species showed no association with natural canopy gaps. Secondly, there was no significant difference in the height of woody sprout regrowth between any of the experimental manipulations of competition following 2 years of fire protected treatment. Furthermore, there were only marginally more saplings in the tree killed treatment compared to the control after 3 years. These results contrast with studies of regeneration in some temperate Australian forest where suppression of regrowth by overstorey trees is pronounced (Incoll 1979, Rotheram 1983, Bowman and Kirkpatrick 1986a) and where regeneration responds quickly to clearfelling (Lockett and Candy 1984).

Nevertheless, other results from this study show that sapling release is promoted by relief from overstorey competition. The clearfelled areas older than 12 years have far greater densities of sapling and pole size trees than the surrounding forest and one of the 2 year old clearfelled blocks at Yapilika developed a stand of *Eucalyptus nesophila* saplings. However, the size class distribution of the regeneration on the old clearfelled plots is not indicative of an even aged stand (Fig. 5.4). The production of sapling stems from the regeneration pool of woody sprouts is intermittent even when conditions are suitable for regeneration.

Overstorey competition does contribute to regrowth suppression. However, it is clear from these results that regeneration is markedly sporadic. The following factors could contribute to the intermittent release of saplings.

1) Potential saplings may be destroyed by fire.

2) Characteristics of individual sites may provide conditions necessary for regeneration.

3) Particular climatic conditions may provide conditions necessary for regeneration.

4) The physiological condition of the underground organs of the woody sprouts may determine their propensity to become saplings. Suitable individuals may occur sporadically.

5) Relief from above-ground herbivory may contribute to sapling success.

6) Tree roots are not necessarily concentrated around their mother stems. Regeneration may be occurring where roots are less concentrated but not necessarily in association with canopy gaps.

The merit of these hypotheses in the light of existing evidence can be reviewed.

Regrowth on the Karslake clearfelled block is more advanced both in terms of the density and median size of regrowth trees than the Pularumpi Road site. These sites have different histories. Firstly the Pularumpi Road site was cleared 1 year later. Secondly the rainfall records of the stations nearest to these two sites (Pularumpi and Milikapiti; Bureau of Meteorology 1988) indicate that the Pularumpi Road site may have slightly higher rainfall than Karslake Peninsula. However, these are minor differences. The major distinguishing feature is that Karslake was fire protected for at least 10 years after establishment and the Pularumpi Road site has been regularly burnt. This suggests that relief from fire in combination with overstorey release does contribute to sapling development on these sites. Lacey and Whelan (1976) attribute differences in *Eucalyptus miniata* regeneration on two clearfelled blocks to the contrasting fire histories of the sites.

Differences in site quality may also contribute to the discrepancy between the Karslake and Pularumpi Road clearfelled blocks. Chapter 4 contrasts the regeneration response on two undisturbed patches of *Eucalyptus miniata-Eucalyptus tetrodonta* forest that have been fire protected for extended periods. Disparate levels of sapling development between the two sites is attributed to edaphic differences and supports the hypothesis that site factors contribute to regeneration potential. Sapling development was sporadic on Howards Peninsula despite substantial removal of overwood by a tropical cyclone (Wilson and Bowman 1987).

Longterm studies would be necessary to determine the influence of irregular climatic events on regeneration. However, there is no evidence that regeneration occurs in specific climatic situations. The adjacent clearfelled blocks at Yapilika have the same climatic history but only one of these blocks developed regeneration.

Plate 5.4 shows sapling *Eucalyptus tetrodonta* regenerating from root suckers. The frequency of this occurrence is not known and regenerating saplings attached to mature trees were never observed by the author. It is possible that underground attachments are severed after sapling development. If the growth of *Eucalyptus tetrodonta* saplings is commonly enhanced by mature trees, it may explain the fact that this species showed no association with canopy gaps. *Eucalyptus miniata* does not regenerate from suckers and was associated with canopy gaps. The tendency for *Eucalyptus miniata* to regenerate where overwood competition is low, and the tendency of *Eucalyptus tetrodonta* regeneration to occur regardless of competition, may be features of the ecology of these species contributing to their niche separation.

Jacobs (1955) has noted that many forest eucalypts have plagiotropic (horizontal growth) stems in their juvenile phase. These stems can be replaced by stems with an erect habit that Abbott and Loneragan (1984) have called "dynamic shoots". This description is appropriate for *Eucalyptus miniata* and the initiation of a dynamic shoot was documented in this study. Abbott and Loneragan (1984) suggest that the dynamic shoots cannot arise from lignotubers less than 15 cm long, which corresponds to an age of 15-20 years. This may relate to their storage capacity. Lignotubers have been shown to contain concentrations of inorganic nutrients and starch in species of *Eucalyptus* (Carrodus and Blake 1970, Mullette and Bamber 1978).

In tropical eucalypt forest some lignotuber features are associated with successful saplings. There is evidence that medium sized (presumably middle aged) lignotubers are most likely to support saplings. Plants with small lignotubers have not developed sufficiently to produce successful saplings. Old plants have large lignotubers and share resources between multiple buds. These plants senesce at an unknown age and large dead lignotubers can be found in these forests (Plate 5.5). These plants do not appear to have supported tree size stems. Thus, juvenile shoots are produced throughout the life of a tree provided a dynamic shoot has never been succesful. Regeneration may be dependent on the presence of a cohort of trees of

Plate 5.4 *Eucalyptus tetrodonta* saplings attached to a rhizome.

Plate 5.5 Dead lignotuber without evidence of having supported tree size stems.

suitable physiological age. Seedling establishment in tropical eucalypt forest is infrequent. This may mean that there are limited trees of suitable age for regeneration when an overstorey gap becomes available.

The presence of a tap root seems to increase the probability of sapling success for *Buchanania obovata, Terminalia ferdinandiana* and *Eucalyptus miniata*. This study examined features of root systems that can be assessed in the proximity of the lignotuber. The extent and condition of root systems may be critical for the switch from suppressed woody sprout to the tree lifeform.

Termites are particularly abundant in the tropical savannas of Australia (Braithwaite *et al.* 1988) as they are in similar environments elsewhere (Josens 1983). Subterranean termites are considerably more abundant than those that live above the soil surface in African savanna (Josens 1983). The excavation of lignotubers during this study revealed they are usually degenerate and suffer a constant barrage of attack from subterranean herbivores. Plate 5.6 shows a tap root that has been destroyed by termites. The extent of this type of damage suggests that the development of tree roots may be limited by these herbivores. Andersen's (1987) recent review postulates that subterranean herbivory is an important and certainly underrated cause of plant stress. Cantor and Whitham (1989) provide evidence that the consumption of aspen roots by pocket gophers limits the distribution of this tree. If underground herbivory limits root development it may be an important determinant of sapling release. Investigations of underground herbivory would be a valuable contribution to our understanding of vegetation dynamics in the tropical savannas of Australia.

It was noted during the monitoring of woody sprout growth that stems exhibited considerable insect damage. There are no quantified studies of insect herbivory from Australian savanna (Andersen and Lonsdale 1990). Chapter 6 attempts to redress this situation with the specific intent of examining the importance of insect herbivory as an influence on vegetation.

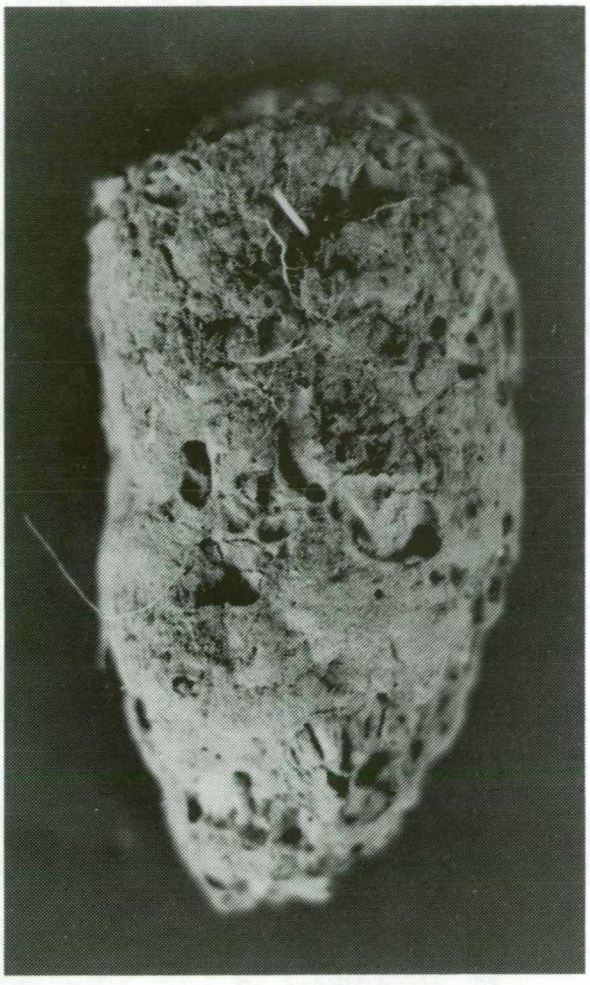


Plate 5.6 Tap root from *Eucalyptus nesophila* destroyed by epigeous termites.

It appears from this study that the influence of tree roots extends at least 25 m from mature forest stems. The magnitude of this influence may not be unusual for Australian forests as Henry and Florence (1966) report that overstorey inhibits regeneration for a distance of at least 30 m in the eucalypt forest of southeast Queensland. Werner (1986) excavated tree roots in tropical eucalypt forest and indicated that tree root biomass is fairly constant with distance from the trunk with maximum biomass occurring at a distance of 5 m from mother stems. Thus, root competition in a typical canopy gap such as that caused by one tree fall may not be substantially lower than elsewhere. This would explain the weak association of saplings and natural canopy gaps at Paru on Melville Island. Areas of ground with low concentrations of roots may be difficult to predict from the distribution of tree stems. Excavation of forest with regenerating saplings would yield valuable information.

The actual mechanism of the competitive influence of overstorey is difficult to determine from the existing evidence. There is clearly an abundance of light in the savanna environment. Projective foliar cover in the eucalypt forest is only about 40% and solar radiation is extremely high in tropical Australia (Budyko 1974) despite yearly fluctuations due to cloud (Kirkpatrick *et al.* 1988). Competition for nutrients seems unlikely given that woody sprouts did not respond to the addition of fertilizer (Section 3.3.5, Wilson 1990). It is difficult to preclude competition for moisture. However, there is some evidence that cannot easily be equated with moisture limitation. Growth of woody sprouts is suppressed despite the availability of ample soil moisture during the wet season (Section 3.3.1). Furthermore, regeneration in the experimental plot without overstorey was negligible despite more favourable deep soil (150 cm) moisture conditions. Medina (1982) and Sarmiento *et al.* (1985) conclude that the deep root systems of tropical savanna trees are able to exploit soil depths that have favourable moisture conditions throughout the year. Section 2.3.3 provides evidence from Melville Island in support of this assessment.

Given that competition for moisture and nutrients does not seem to explain overwood suppression then attention should be given to

allelopathic interference. This phenomena has been clearly demonstrated for the tree genus *Eucalyptus* (Florence and Croker 1962, Evans *et al.* 1967, del Moral and Muller 1969, 1970, Al-Mousawi and Al-Naib 1975, Ashton and Willis 1982, Bowman and Kirkpatrick 1986b, Suresh and Vinaya Rai 1988). Thus the suppressive effects of leaf and litter leachates and root chemicals and soil microbial associations in these forests would seem to be fruitful avenues for future investigations.

5.4.2 Can forest structure be maintained under present conditions?

It is possible to discuss the perpetuation of forest structure using assumptions regarding sapling (>2 m H, <10 cm dbh) and tree (>10 cm dbh) longevity. The tree rings of a 40 cm dbh tree indicated an age of 60 years (Mucha 1979). From dendrochronological and historical evidence collected near Darwin and on Melville Island, Mucha (1979) concluded that eucalypt trees rarely live to 100 years in the monsoon tropics. This is a short life compared to other species of *Eucalyptus* in temperate Australia. Termite damage may be the cause of their relatively short life. The absolute age of trees is greater than suggested by Mucha because they may exist for many decades as woody sprouts.

Eucalyptus miniata shows a greater disparity between saplings and trees than other species (Fig. 5.1). The assumptions regarding replacement of overstorey canopy will be demonstrated with the stand structure information for this species (Fig. 5.1). Using Mucha's (1979) evidence the assumption shall be made that tree stems die at 80 years and exist for 72 years larger than 10 cm dbh. There are 84 *Eucalyptus miniata* trees per ha greater than 10 cm dbh in a typical open forest on Melville Island (Fig. 5.1). This means that an average of 1.2 *Eucalyptus miniata* trees will die per ha per year. There are 7.1 sapling stems per ha (Fig. 5.1). Assuming the oldest saplings are 8 years old then 0.9 saplings per ha are released from the ground layer per year. Even if all of these saplings survive recruitment will fall short of mortality.

The above calculation determines that 31.5% of *Eucalyptus nesophila* saplings and 19.2% of *Eucalyptus tetrodonta* saplings must survive if the canopy is to be sustained. Werner (1986) suggests that trees live

longer than 100 years in the tropical eucalypt forest. If she is right and Mucha is wrong, the mortality rate would be lower than assumed here and recruitment levels from the ground layer need not be as high as suggested by the calculation presented above.

The release of saplings from the ground layer occurs sporadically even with appropriate conditions and there is a propensity for this limited recruitment to occur where competition is low. Thus mortality is reduced in the early stages of tree development. It seems individuals that are suitable as canopy trees are selected before the sapling lifestage.

If a tree species suffers decline during a generation, one of the other dominant tree species may become relatively more frequent in the canopy. There is evidence that switches in relative overstorey dominance does occur. The clearfelled block at Karslake has sparse *Erythrophleum chlorostachys* regeneration despite this species being an important canopy dominant in the original forest. The reverse situation is occurring at the Pularumpi Road site where *Erythrophleum chlorostachys* seems to be more abundant in the developing stand than it was in the original forest. These sites had different fire histories. Features of the regeneration niche such as the size of the canopy gap and fire history may contribute to the composition of the regenerating stand.

Eucalyptus miniata is the most dominant tree species at Paru. However, the population structure of this species suggests that it has the least potential of maintaining its present densities. If *Eucalyptus miniata* declines canopy structure can still be maintained because reduced density of this species will be compensated by increases in the other overstorey trees. It appears that a regeneration event favoured the accession of *Eucalyptus tetrodonta* in the near past because there is a peak in abundance of small trees of this species. The relatively high frequencies of small *Eucalyptus tetrodonta* trees seems to suggest that large trees of this species will become relatively more abundant as the forest develops through the generation time of the existing trees.

This discussion suggests that mortality of developing trees is relatively low. Furthermore, there is evidence that temporary

declines in the relative dominance of one tree species will be compensated by increases in another species. These facts suggest that forest structure will be maintained under present conditions.

CHAPTER 6 PHYTOPHAGOUS INSECT/VEGETATION INTERACTIONS IN TROPICAL EUCALYPT FOREST

6.1 Introduction

Generally insect grazing decreases primary production (Kulman 1971, Crawley 1989) although Mattson and Addy (1975) suggest that low grazing intensities can increase production in some forests and there are numerous examples of this phenomenon from agricultural systems (see review by Harris 1974). For eucalypts, the detrimental effect of insect grazing on growth has been demonstrated both in terms of episodic outbreak (Readshaw and Mazanec 1969, Morrow and Le Marche 1978) and experimental protection using insecticide (Greaves 1966, Lowman and Heatwole 1987).

There has been some evidence of insect grazing activities influencing vegetation succession (Coley 1983, Brown 1984, Brown and Gange 1989, Gibson *et al.* 1987), and discussion (Chilvers and Brittain 1972, Morrow 1977a, Hodkinson and Hughes 1982) and evidence (Burdon and Chilvers 1974a, Bentley and Whittaker 1979) of insect herbivory influencing other vegetation characteristics such as structure and community composition.

Determining the effects of insects on plants is difficult because interactions between these components of the biota are often multi-directional. Characteristics of season (Janzen 1973, Frith and Frith 1985), vegetation structure (Schowalter *et al.* 1981), plant growth (Reichle *et al.* 1973, Lowman 1985), species composition (Coley 1983) and moisture stress (White 1969, Wearing and van Emden 1967) have all been correlated with the abundance of insects which makes the direction of insect-vegetation interactions difficult to decipher.

It is possible that some of the spatial and temporal vegetation patterns in the eucalypt forest on Melville Island may be attributed to the activity of insects. The transects presented in Chapter 2 describe the community relations of common tree species of Melville Island's savanna forest. This study and the study presented in Chapter 3

demonstrated that some tree species occur in communities with particular moisture and nutrient regimes. However, determining the environmental controls across the gradient from evergreen forest to semi-deciduous low forest proved difficult. It has been shown in experimental situations that stress, as inflicted by the availability of nutrients (see references in Dale 1989) and moisture (see references in Holtzer *et al.* 1989) can affect the susceptibility of plant species to insect attack. It is possible that environmental conditions affects the susceptibility of plants to insects and this may have bearing on the relative success of tree species.

Chapter 5 highlighted an important enigma that is critical to understanding the regeneration process in tropical eucalypt forest. The problem is why the growth of woody sprouts does not occur in concert with optimum soil moisture conditions. The midstorey in the forest is sparse although there is a mass of short woody stems of many tree species present in the ground layer. These suppressed woody sprouts include the overstorey species and other tree species that only rarely reach the canopy.

During a study that monitored the growth of woody sprouts it was observed that foliage and stems were necrotic and insect damaged (Chapter 3)(see also Andersen and Lonsdale 1990). The intensity of insect grazing was suggested as a possible explanation for the stunting of woody sprouts. Insects are invariably more abundant during the wettest part of the year in the seasonal tropics (see for example Janzen 1973, Bigger 1976, Gillon Y. 1983, Wolda 1989). The avoidance of wet season herbivory may contribute to the paradox whereby growth is out of kilter with available soil moisture.

The present study examines the influence of season, host species and plant community on insect abundance and grazing intensities and seeks to establish the merits of the following hypotheses which flow from the questions defined in Chapter 3:

1) Insect herbivory inhibits the development of young trees by inhibiting the growth potential of ground layer tree stems.

2) Dormancy of woody sprouts coincides with peaks in the abundance of phytophagous insects.

3) Canopy species are less damaged than tree species confined to the ground layer in any particular community.

To address these hypotheses this study seeks to describe seasonal patterns of insect grazing along an environmental gradient that involves shifting dominance of tree species.

If insects do influence forest structure and growth characteristics it would be interesting to know: 1) the groups of phytophagous insects which are causing damage; 2) the times of the year these groups are most abundant; 3) the degree of specificity between phytophagous insects and their hosts; 4) whether specificity is host species or habitat orientated.

To answer these questions the structure of the insect community was investigated as it relates to host plant species, vegetation type and season. Damage inflicted by sucking insects is not readily apparent but has been shown to affect growth in agricultural systems (Morrill *et al.* 1984, Breen and Teestes 1986). Because the effect of these insects is difficult to assess the abundance of sucking insects is used as a surrogate for the damage they cause in the present study.

If insects cannot be held responsible for vegetation characteristics then insect grazing and population structure information is of intrinsic interest to the scientific community, and studies documenting phytophagous insect activity are noticeably lacking from savanna of the monsoonal tropics (Gillon Y. 1983, Andersen and Lonsdale 1990).

It has been argued that vertebrate consumers have the potential to influence vegetation characteristics to a greater degree than their invertebrate counterparts (Crawley 1989). The eucalypt forest of Melville Island are especially suited to studies of insect/plant interactions because the affects of vertebrate herbivores are minimal. Densities of native and feral animals are low and it has been observed by the author following intensive monitoring of growth that vertebrate browsing of woody sprouts is negligible.

6.2 Methods

6.2.1 Insect damage

Field methods

The evergreen forest and semi-deciduous low forest monitored for the growth of woody sprouts (Section 3.2.1), near Paru on Melville Island, provided the study sites (transect 4, Fig. 2.11). The forest is dominated by *Eucalyptus miniata* with *Eucalyptus tetrodonta* and *Eucalyptus nesophila* as canopy sub-dominants. The low forest is dominated by *Eucalyptus latifolia* with *Eucalyptus confertiflora* and *Erythrophleum chlorostachys* as sub-dominants in the upper canopy. *Terminalia ferdinandiana* forms a sparse layer in the mid-canopy of the semi-deciduous low forest. *Buchanania obovata, Planchonia careya, Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus confertiflora, Acacia aulacocarpa, Eucalyptus tetrodonta* and *Eucalyptus miniata* were monitored in the forest and the first six of these species were monitored in the low forest. *Eucalyptus miniata* and *Eucalyptus tetrodonta* were absent from the low forest. Three (or all, if less were present) stems from 15 individuals of eight species were tagged in mid-August 1987.

Lowman (1984) found that discrete sampling of insect damage can considerably underestimate actual damage and a monitoring procedure was adopted to allow for leaves whose complete absence could be attributed to insects. Individuals plants were located using the procedure outlined in Chapter 3. The leaves of each tagged stem were permanently marked using a waterproof felt pen by writing small numbers on their adaxial surface and were sequenced from the base of the stem to the apical bud. The leaves of branches were numbered as hundredths of the leaf on the main stem from which the branch arose. Thus, the first leaves of a branch from the axil of the fourth leaf were numbered 4.01, 4.02, 4.03....etc.

The first 100 leaves of each species were measured and thereafter leaf lengths were estimated to the nearest centimetre. For the bipinnate leaves of *Erythrophleum chlorostachys* leaf size was assigned to an

ordinal score from 1-10. The amount of damage for each leaf was estimated according to the classes <1, 1-10, 10-25, 25-50, 50-75 and 75-100% in the following categories: a) chewing damage (entire sections of the leaf eaten); b) distorting damage, a category including psyllid spots, distortion caused by damage to vascular tissue from sucking insects and leaf galls (Plate 6.1); c) mining damage, where mesophyll tissue has been consumed and the epidermis remains intact (Plate 6.2); d) other damage, which includes types of leaf damage apparently not caused by insects such as senescent necrosis.

There are some problems with insect damage assessment that should be detailed. Leaf holes enlarge proportionately with leaf expansion (Reichle *et al.* 1973, Lowman 1987), thus small holes that have increased their size will be assessed as a greater loss than actually occurred. A leaf portion may die because vascular tissue has been severed by insects and using the method of this study will be identified in the 'other' damage category. These problems with damage assessment are difficult to avoid.

New leaves were numbered and all leaves assessed for subsequent damage at the end of the dry season (17-23/11/87), at the end of the following wet season (5-11/4/88) and just prior to the sites being burnt in the second dry season (7-13/6/88). In this manner more than 22,000 leaves were assessed and processed.

As this fieldwork was being conducted it was evident that many individuals suffered significant stem damage. This damage type was assessed for each of the sampled species by assigning every stem of 20 individuals at each site to one of the following arbitrary categories on 16/11/88. 1) no visible damage; 2) less than ten minor lesions per 10 cm stem length; 3) between 10 and 30 minor lesions per 10 cm stem length or one major gall or lesion per stem; 4) more damage than 3.

Analytical methods

The area of about 30 intact leaves covering the range of sizes of the eight measured tree species were measured. A leaf area scanner that measures the interruptions between tightly packed electronic signals

on a cathode tube performed this task. The relationship between leaf length and area was determined using Cricketgraph®, a computer package that fits functions to data points. This procedure allowed calculation of an absolute measure of leaf area consumed. The defined formulae were as follows:

Buchanania obovata:	$A=-14.9+2.68L+0.37L^2-0.008L^3$; R=0.98
Planchonia careya:	$A=0.59L^{1.85}$; R=0.98
Terminalia ferdinandiana:	$A=0.5L^{1.89}$; R=0.99
Erythrophleum chlorostachys:	$A=34.05L^{1.37}$; R=0.91
Eucalyptus tetrodonta:	$A=0.76+1.85L^2+0.105L^3$; R=0.93
Eucalyptus miniata:	$A=0.48L^{1.89}$; R=0.98
Eucalyptus confertiflora:	$A=-26.6+7.1L^2+0.17L^3$; R=1.0
Acacia aulacocarpa:	$A=2.3x10^{(0.092L)}$; R=0.97

where: A=leaf area; L=leaf length or ordinal size score for *Erythrophleum chlorostachys*.

Despite the progressive monitoring of individual leaves using this technique it was difficult to determine whether insect damage was the cause of a leaf's disappearance. A computer program was developed that differentiated between leaves excised by insects and other causes. If the oldest leaves (those not preceded by existing leaves) are absent then it was assumed that excision was not prompted by insect damage. If absent leaves are preceded on the plant by older leaves and at the previous sampling time had insect related damage greater than 60% then excision was attributed to insects. The size of the excised leaf was assigned to the mean leaf size for that particular species and the damage assigned to damage classes in the same proportion as for the previous sampling period and totalling 100 percent. All missing leaves, including those that were preceded by older leaves but did not meet the 60% criteria and those that were not preceded by older leaves, were assigned to the size and damage values equal to the previous sampling period. This was done so that damage at a particular time was a measure of total damage since post-fire emergence and was necessary in order that damage determinations for a particular time frame were not overestimated. This estimate of damage will be called the longterm estimate and is opposed to discrete measures which are

single measures determined from one time (Landsberg 1989). In order to make the data set completely cumulative a second program inserted damage values of fallen old leaves (not preceded by current leaves) from the previous sampling time. A third program subtracted damage values of each stem from the values at the subsequent sampling time which allows determination of the amount of insect damage occurring between any two sampling periods. Damage that removes new leaves between sampling periods would be evident from leaf scars and was insignificant for all species.

Extension growth over each period was calculated by subtracting the height at the beginning of the period from the height at the end of that period.

The following measure of insect damage was used for statistical treatment between season, plant community and plant host species:

$$D = \frac{C}{t \times A}$$

where: C=area of leaf material consumed over sampling period; t=time of sampling period; A=area of leaf material available at the beginning of the sampling period.

This measure of insect damage overcomes the problems of other measures such as percentage damage or leaf area consumed, both of which are probably dependent on the amount of leaf area available, which increases as the plants grow. However, D is not standard between time periods and will be proportionately overestimated during periods of active growth. During these phases more plant material becomes available to insects than is available at the beginning of that sampling period (A).

Analysis of variance was used to examine the effect of season, plant community and plant host species on D following a $\log_n(x+1)$ transformation. Three separate analyses of variance were performed: a one-way ANOVA by plant species; a two-way ANOVA by plant community and season; and a three-way ANOVA by season,

community and plant species with values for *Eucalyptus miniata* and *Eucalyptus tetrodonta* excluded. This combination of tests was necessary because *Eucalyptus miniata* and *Eucalyptus tetrodonta* were absent from the low forest.

All subsequent analyses were performed on the individual damage categories and their totals. Extension growth and the total area damaged by insects for each period were divided by the number of days for that period. These damage and growth coefficients for the individual stems of each species were then compared using Pearson's product moment correlation coefficient. The relationship between height and number of stems and percentage insect damage after 1 year's growth was also explored using correlation. For species occurring at both sites percentage damage differences for all times were compared between sites using the Mann-Whitney U-test. The relationship between general senescence ('other damage' category) and the extent of insect damage at the end of the wet season and final sampling periods was explored using correlation.

Stem damage was compared for species occurring at both sites using the Mann-Whitney U-test.

6.2.2 Insecticide experiment

Field methods

Fifteen individuals of the eight assessed species were tagged and measured soon after post-fire emergence (mid-August 1987) in *Eucalyptus miniata* forest nearby and similar to that sampled for damage assessment. The individuals were sprayed with an equal mixture of the systemic insecticide Lorsban® (active ingredient: Chlorpyrifos) and the surface acting chemical Rogor® (Dimetholate) at approximately 10 day intervals. A replicate plot was established at a nearby site and the individuals sprayed with water to determine whether the quantity of water that was applied during spraying enhanced growth.

This procedure was maintained until 24 November of the same year, by which time it was obvious that the insecticide mixture was toxic for some species. The stems of all plants were measured at this time. The insect damage of plants in the sprayed plot was assessed using the method outlined for damage monitoring except that the sample was a discrete measure with no account of missing leaves.

Analytical methods

From the seasonal assessment a discrete measure of damage was extracted from the late November sampling of the *Eucalyptus miniata* forest to serve as an insect damage control. The mean total insect damage and other damage for all the leaves of each stem was calculated and these data compared with the same data from the insecticide sprayed plot using the Mann-Whitney U-test. The 'other' damage class included the phytotoxic effect of the insecticide which was evident as brown dead areas distinct from types of damage witnessed elsewhere. The influence of damage protection on the growth of species was determined following application of a formula that allows for differences in initial plant size to provide a measure of relative growth rate (R):

$$R=100(\ln h_1-\ln h_0/t);$$

where: h_1=plant height at final measurement, h_0=plant height at initial measurement, t=time$_{1-0}$ (Radford 1967).

The R values of the tallest stem were compared between the treatments, for each tree species, using the Mann-Whitney U-test.

6.2.3 Phytophagous insect community

Sampling procedure

Insects were collected in the *Eucalyptus miniata* forest and the *Eucalyptus latifolia* low forest from areas around the insect damage assessment plots. Samples were taken during the middle of the periods between damage assessment samples: the late dry season (early

September 1987), the mid wet season (mid-January 1988) and the early dry season (mid-May 1988). Woody sprouts were approached carefully and gently searched for phytophagous insects which were collected from plant surfaces using an aspirator. The plants were then beaten over a 100 x 75 cm frame stretched with white canvas and the fallen insects were collected in the aspirator. The identity (using code names pertaining to individual species) of escapees was determined where possible. Plant stems were measured after sampling. Caterpillars were counted and assigned to their habitation of cocoons or plant surfaces. At each time and site the sampling procedure was carried out for 20 woody sprouts of each of the species assessed for damage.

Sweep sampling was also conducted to provide adequate representation of the more agile insect species. A 50 cm sweep net with a 1.5 mm mesh size was passed once through the foliage of twenty woody sprouts of each species at each site and time. The same sweeping procedure was repeated at night between the hours of 11 pm and 3 am. Plant species were identified under torchlight during collection of the night sample.

A wet season sample was collected from the eight forest tree species in similar vegetation to the *Eucalyptus miniata* forest site using identical methods to those outlined above. This forest was 30 km distant, near Milikapiti, and was sampled to get an indication of spatial pattern within one vegetation type.

The determination of phytophagous status was unequivocal for most insects. However, some families, particularly in the Orthoptera, have species with a range of feeding strategies (CSIRO 1970). Given that all insects were collected from live plant surfaces, the few doubtful cases were assumed to be phytophagous. Non-phytophagous were not included in this study.

Insects were sorted to morphospecies. This was possible even for the particularly abundant juvenile Homoptera. Individuals were counted in each sample and the species were identified to family for most groups and to subfamily for beetles. Identifications were made by the author and a cross-section of the taxa were viewed by specialist

taxonomists for verification. The collection is lodged with the CSIRO Tropical Ecosystem Research Centre (Darwin).

Analytical methods

The relationship between stem length and leaf weight was determined by measuring, oven drying (105° C for 48 hours) and weighing 20-30 stems of each of the sampled species (collected in October). A time decay function (approximately derived from the insect damage levels) was included that allowed for the depletion of biomass through herbivory. The functions relating stem length and time to biomass are as follows:

Buchanania obovata	$M=0.9938^{t}(0.016S^{1.904})$; R=0.91
Planchonia careya	$M=0.9888^{t}(0.008S^{1.881})$; R=0.94
Terminalia ferdinandiana	$M=0.9806^{t}(0.007S^{2.076})$; R=0.90
Erythrophleum chlorostachys	$M=0.9819^{t}(0.117S^{1.531})$; R=0.90
Eucalyptus tetrodonta	$M=0.9894^{t}(1.790x10^{0.014S})$; R=0.94
Eucalyptus miniata	$M= 0.9913^{t}(0.001S^{2.383})$; R=0.94
Eucalyptus confertiflora	$M= 0.9819^{t}(0.005S^{2.179})$; R=0.89
Acacia aulacocarpa	$M= 0.9925^{t}(0.0133S^{1.660})$; R=0.94

where: M=dry weight; S=stem length; t=time (months).

Further analysis was performed on the densities of insects per kg of dried plant material. For most analyses the individual species were aggregated according to their major insect group:- bugs [Hemiptera: separated into psyllids (from the superfamily Psylloidea) and Other hemiptera; grasshoppers and crickets (Orthoptera), beetles (Coleoptera) and caterpillars (Lepidoptera). The samples of the individual plants were pooled so that insects collected from a plant species at one time from a particular vegetation type became the sampling unit. Insects from the night sample were not included. The wet season insect samples were compared between the *Eucalyptus miniata* forests for each individual host species using the Mann-Whitney U-test. Where it was necessary data was appropriately transformed using a $\log_n(x+1)$ or square root transformation in preparation for ANOVA. The following analyses were performed on the day samples: three-way

ANOVA with lifeform (eucalypts, acacias and other trees), season and community as the treatment groups; two-way ANOVA with season and community as the treatment groups; one-way ANOVA with host plant species as the treatment group; and a three-way ANOVA with samples from *Eucalyptus miniata, Eucalyptus tetrodonta* and *Terminalia ferdinandiana* removed from the data set. This multiplicity of tests was necessary because *Eucalyptus miniata* and *Eucalyptus tetrodonta* were not present in the low forest and *Terminalia ferdinandiana* could not be sampled during the late dry season because it had barely emerged from the ground. Results can be interpreted by looking for consistencies between these tests. Inconsistencies suggest that indeterminant interactions between treatment classes have important effects on insect abundances.

ANOVA was repeated in the same way for individual insect species recorded nine or more times. This analysis included the individuals collected during the night sample. Host specificity was further examined using Morrow's (1977b) scheme that ruled insect species with 80% or more of their individuals on one host plant as host specific.

One set of 20 sweeps was the sampling unit for a comparison between day and night insect abundances. Insect groups were compared using the Mann-Whitney U-test.

6.3 Results

6.3.1 Insect damage

Damage levels after a year of post-fire emergence are presented in Table 6.1. Total insect damage varied from 7.8% for *Buchanania obovata* and *Terminalia ferdinandiana* in the forest to 43.2% for *Acacia aulacocarpa* in the low forest. The mean values across species were 17.1% in the forest and 22.3% in the low forest. Many of stems were severely damaged by insects that suck, eat and hive in their stems. This was particularly obvious on *Eucalyptus tetrodonta, Eucalyptus miniata* in the forest and *Eucalyptus confertiflora* in both forest and low

Table 6.1 Mean (and s.e.m.) insect damage (% of total leaf area) for each damage class and combined totals according to plant species and vegetation type after one year's post-fire emergence.

Forest	Chewing damage		Distorting damage		Mining damage		Other damage		Total insect damage		Total damage	
	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.
Buchanania obovata	5.8	1.7	2.0	1.0	0.0	0.0	3.8	0.8	7.8	2.0	11.6	2.3
Planchonia careya	15.7	2.3	0.8	0.3	0.1	0.1	11.7	1.8	16.6	2.5	28.3	3.0
Terminalia ferdinandiana	7.0	1.5	0.0	0.0	0.7	0.6	17.2	1.6	7.8	1.6	24.9	1.9
Erythrophleum chlorostachys	13.2	2.3	0.3	0.2	1.6	0.5	11.2	1.5	15.1	2.3	26.2	2.2
Eucalyptus tetrodonta	10.9	1.9	0.7	0.3	3.1	1.0	10.2	1.6	14.7	2.0	24.9	2.5
Eucalyptus miniata	15.4	2.7	2.4	0.6	0.6	0.4	16.0	2.6	18.4	3.3	34.4	5.3
Eucalyptus confertiflora	30.3	4.0	0.2	0.1	8.7	1.6	1.1	0.8	39.2	4.4	40.3	4.3
Acacia aualcocarpa	11.9	1.5	0.1	0.1	5.5	1.3	8.9	2.1	17.5	1.8	26.5	2.5
All species	13.7	2.7	0.6	0.3	2.9	1.1	10.0	1.9	17.1	3.5	27.1	3.0
Low forest												
Buchanania obovata	6.3	1.4	0.4	0.2	5.1	2.0	2.7	0.5	11.8	2.3	14.5	2.2
Planchonia careya	9.1	1.1	0.3	0.1	0.4	0.2	6.8	1.1	9.8	1.2	16.6	1.5
Terminalia ferdinandiana	13.0	3.1	0.4	0.3	0.0	0.0	15.7	1.7	13.5	3.1	29.2	2.9
Erythrophleum chlorostachys	17.9	1.8	0.0	0.0	3.1	1.0	9.7	1.4	21.1	2.1	30.8	2.0
Eucalyptus confertiflora	14.7	3.0	1.3	0.9	18.2	3.5	4.7	2.8	34.2	4.6	29.0	4.6
Acacia aualcocarpa	28.1	3.7	0.0	0.0	15.1	2.8	0.0	0.0	43.2	4.7	43.3	4.6
All species	14.7	3.2	0.4	0.2	7.0	3.2	6.6	2.3	22.3	5.5	28.9	3.0

forest where 20.0, 35.5, 75.0 and 26.0% of stems were moderately to severely damaged (class 2 and 3) respectively, after 4 months post-fire emergence.

Appendix 4 portrays the mean condition of woody sprouts during the year of post-fire emergence in terms of the different insect damage classes. Appendix 4 includes graphs of the mean leaf area per plant damaged by insects. Chewing and mining can be difficult to distinguish in the field because leaf remains disintegrate from old mining damage. However, the sum of chewing and mining damage usually accounts for over 90% of the measured insect damage by the end of the post-emergence year. Exceptions to this generalization were *Buchanania obovata, Eucalyptus tetrodonta, Eucalyptus miniata* in the forest and *Terminalia ferdinandiana* in the low forest where these damage types were less than 90% but account for the vast majority of damage (Table 6.1).

There were significant interactive effects of community, season and plant species on the proportion of leaf area consumed relative to the amount of leaf area available (D). From the three analyses of variance performed some general patterns can be described (Table 6.2). *Eucalyptus confertiflora* seems to be a particularly favourable food source for insects. *Buchanania obovata* and *Terminalia ferdinandiana* are the least favoured species (Table 6.2a). Values of D were higher in the forest than the low forest except during the wet season when values were roughly equal (Table 6.2b and c). Furthermore, values of D were higher in the forest than the low forest for all individual species with the exception of *Acacia aulacocarpa* which had higher values of D in the low forest (Table 6.2c). Generally values of D were depressed during the wet season in both forest types (Table 6.2b) and for most species (Table 6.2c) D seems particularly high during the early dry season relative to other periods. This result is especially prominent because this is a period of growth dormancy and D would be underestimated relative to periods of active growth such as the late dry season period.

Table 6.2 Mean values for the proportional damage term (D) and three separate analyses of variance using plant host species, season and plant community as treatment groups.

a) One-way ANOVA by plant species

	F- value
Plant species	12.43***

Mean D values

Buchanania obovata	*Planchonia careya*	*Terminalia ferdinandiana*	*Erythrophleum chlorostachys*	*Eucalyptus tetrodonta*	*Eucalyptus miniata*	*Eucalyptus confertiflora*	*Acacia aulacocarpa*
0.13	0.23	0.11	0.21	0.24	0.20	0.54	0.28

b) Two-way ANOVA by season and plant community

	F- value
Season x Plant community	5.23***

Mean D values

	Post emergence	Late dry	Wet	Early dry
Forest	0.35	0.21	0.15	0.43
Low forest	0.16	0.18	0.16	0.31

*** P<0.001, ** P<0.01, * P<0.05

Table 6.2 continued

c) Three-way ANOVA by season, plant community and plant species. Species occurring only in one community have been removed.

	F- value
Season x Community	6.09***
Season x Species	2.95***
Community x Species	6.45***
Season x Community x Species	NS

Mean values

	Post emergence	Late dry	Wet	Early dry
Forest	0.39	0.20	0.16	0.49
Low forest	0.16	0.18	0.16	0.31

	Buchanania obovata	*Planchonia careya*	*Terminalia ferdinandiana*	*Erythrophleum chlorostachys*	*Eucalyptus confertiflora*	*Acacia aulacocarpa*
Post emergence	0.18	0.16	0.11	0.10	0.63	0.21
Late dry	0.09	0.13	0.07	0.22	0.41	0.36
Wet	0.12	0.16	0.07	0.19	0.18	0.22
Early dry	0.13	0.46	0.21	0.30	0.94	0.34

	Buchanania obovata	*Planchonia careya*	*Terminalia ferdinandiana*	*Erythrophleum chlorostachys*	*Eucalyptus confertiflora*	*Acacia aulacocarpa*
Forest	0.16	0.37	0.13	0.25	0.68	0.22
Low forest	0.09	0.10	0.09	0.19	0.40	0.34

*** P<0.001, ** P<0.01, * P<0.05

Further insights into interactions between plant growth and phytophagous insect activity can be gleaned by considering the pairs of graphs in Fig. 6.1 concurrently. This information needs to be considered in the light of the seasonal growth of woody sprouts which generally occurs in the late dry season after burning. Little or no growth occurs during the wet season and the early part of the following dry season (Chapter 3).

Eucalyptus tetrodonta in the forest, *Erythrophleum chlorostachys* in the low forest and *Eucalyptus confertiflora* in both communities suffer most during the dry season. *Erythrophleum chlorostachys* in the forest is losing leaf area at the most rapid rate during the wet season but compensating for losses during that period by more sustained leaf production and expansion than other species were capable. Thus, the damage condition of *Erythrophleum chlorostachys* has a similar seasonal pattern in both communities but the pattern of leaf consumption is different between the vegetation types. This notion is consistent with the more sustained wet season growth for the woody sprouts of *Erythrophleum chlorostachys* in the forest relative to other species in any vegetation type (Section 3.3.1). The decay of *Eucalyptus miniata* increases steadily despite peaks in leaf consumption when biomass is low soon after emergence and during the dormant growth phase of the wet season. *Buchanania obovata* and *Acacia aulacocarpa* exhibit disparate patterns of decay between the forest and the low forest. *Acacia aulacocarpa* in the forest suffers the greatest leaf loss during the dry season. In the low forest consumption seems to mirror the availability of resource. Thus, consumption increases as plants grow late in the dry season and remains relatively constant during the wet season. However, the generally smaller size of *Acacia aulacocarpa* in the low forest means that the levels of consumption lead to relatively high damage levels by the end of the sampling period. *Buchanania obovata* in the forest suffers peak damage soon after emergence and little damage during this period in the low forest. However, patterns reverse towards the end of the post-emergence year so that for this species more leaf material is being consumed in the low forest than the forest. *Eucalyptus confertiflora* and *Buchanania obovata* in the forest are targeted during the first post-emergence months. *Eucalyptus confertiflora* in the low

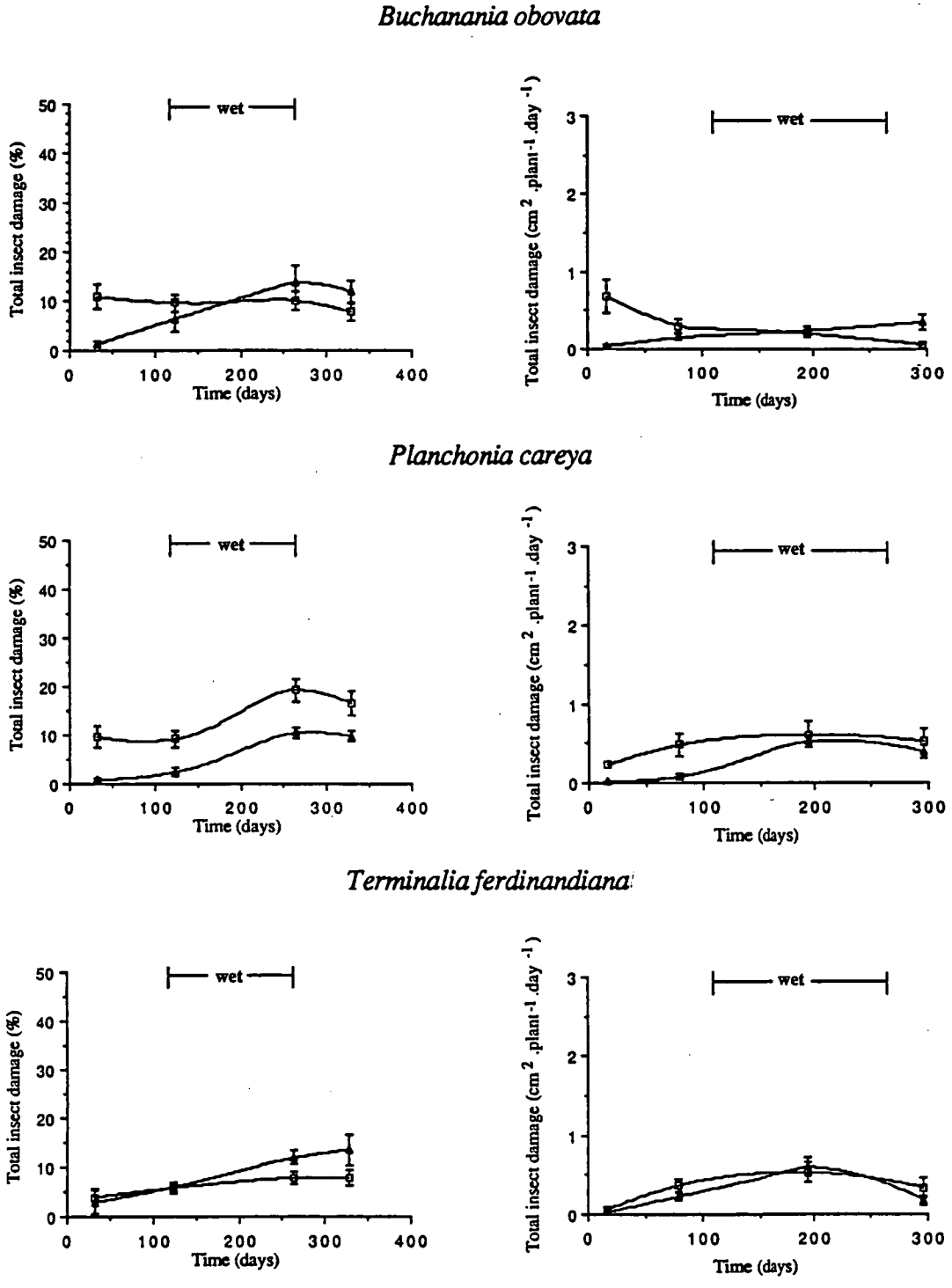
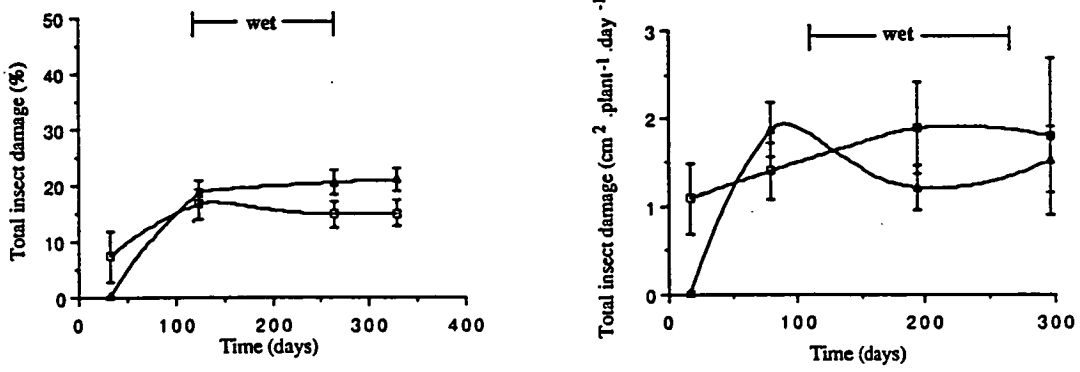
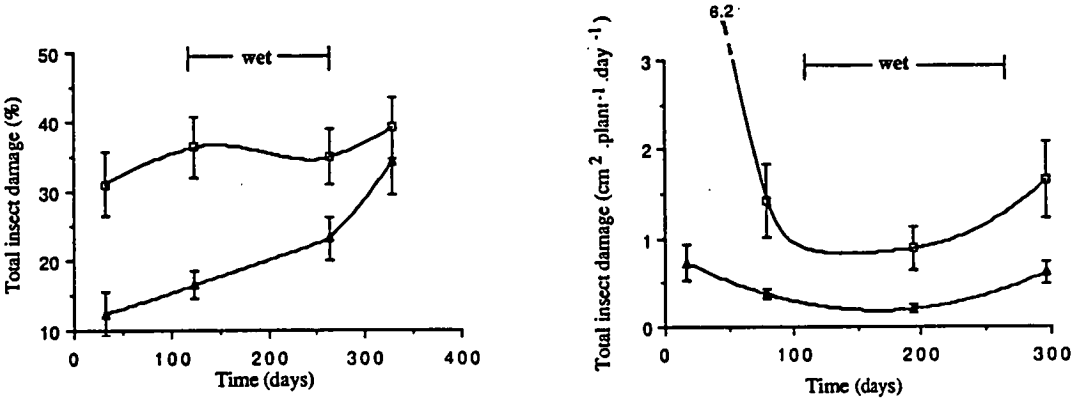


Figure 6.1 Mean (and s.e.m.) total insect damage, in terms of the damage condition of the plant and rate of leaf consumption for eight tree species in two vegetation types (□ forest, ▲ low forest). The wet season period is indicated.

Erythrophleum chlorostachys



Eucalyptus confertiflora



Eucalyptus miniata

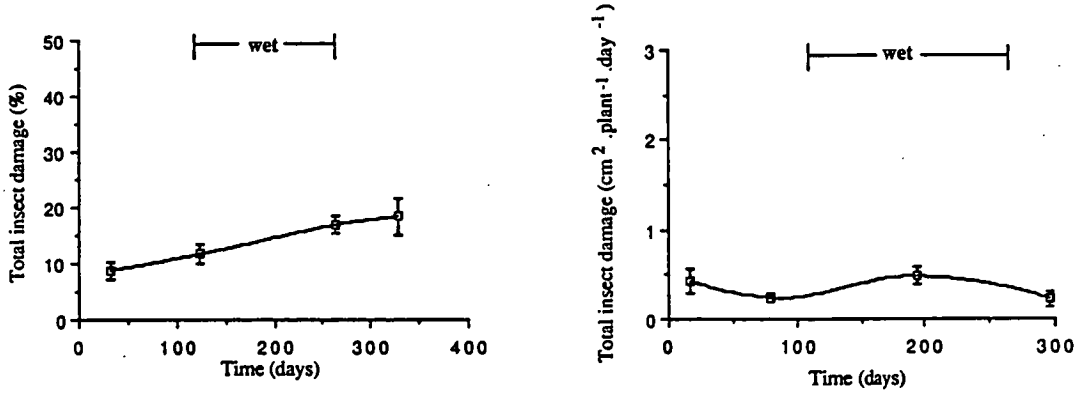


Figure 6.1 continued

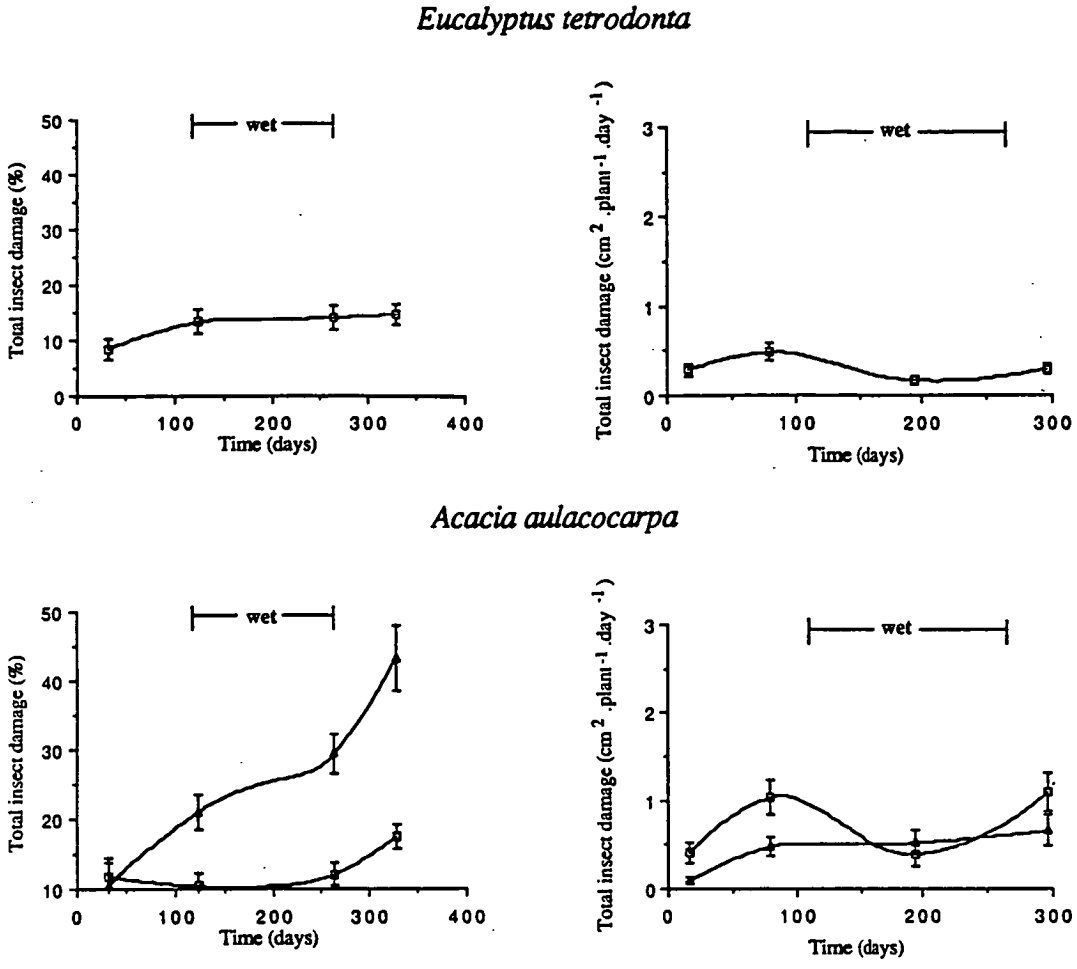


Figure 6.1 continued

---

forest suffers steady rates of consumption which were not compensated by leaf production. By the end of the post-emergence year *Eucalyptus confertiflora* is suffering relatively high damage in both forest communities (Table 6.1).

The absence of significant negative correlations between growth and damage (Table 6.3) suggests that plant growth is not successfully tuned to avoid periods of intense insect grazing.

Table 6.3 Pearson's product moment correlation coefficients between growth rate and damage for the post-emergent year.

Forest	Chewing damage	Distorting damage	Mining damage	Other damage	Total insect damage	Total damage
Buchanania obovata	0.214*	0.289**	0.175	-0.078	0.382***	0.359***
Planchonia careya	0.014	0.362***	0.041	-0.160	0.068	-0.017
Terminalia ferdinandiana	0.259**	0.159	0.003	0.006	0.239*	0.150
Erythrophleum chlorostachys	0.346***	0.098	-0.122	-0.192	0.338***	0.223*
Eucalyptus tetrodonta	0.321***	0.341***	0.173	-0.108	0.394***	0.179
Eucalyptus miniata	0.272**	0.315***	0.292**	-0.022	0.335***	0.270**
Eucalyptus confertiflora	0.751***	-0.093	-0.124	-0.119	0.734***	0.732***
Acacia aualcocarpa	0.269**	0.025	0.139	-0.157	0.287**	0.167
Low forest						
Buchanania obovata	-0.016	0.007	-0.112	-0.088	-0.068	-0.093
Planchonia careya	-0.026	0.187	0.127	-0.253**	0.019	-0.170
Terminalia ferdinandiana	0.314**	0.022	0.108	0.114	0.319**	0.226*
Erythrophleum chlorostachys	0.136	0.168	-0.134	0.064	0.087	0.099
Eucalyptus confertiflora	0.455***	0.217*	-0.022	-0.080	0.406***	0.377***
Acacia aualcocarpa	0.193	-0.094	0.140	0.103	0.205*	0.208*

*** P<0.001, ** P<0.01, * P<0.05

For the species occurring at both sites, the differences in damage between vegetation types is idiosyncratic for particular species and types of damage (Table 6.4, Fig. 6.1). In terms of total insect damage *Buchanania obovata, Planchonia careya* and *Eucalyptus confertiflora* seem to suffer more in the forest than the low forest, while *Terminalia ferdinandiana* and *Acacia aulacocarpa* show the reverse trend. For *Erythrophleum chlorostachys* the relative condition of the plants in the two forest communities switches through time. There does not seem to be any consistent relationship between a species' propensity to reach upper canopies in a particular community and lower levels of insect damage. *Eucalyptus confertiflora* is less damaged during the first post-emergence year in the low forest where this species occurs as a dominant tree. The reverse relationship is evident for *Terminalia ferdinandiana* which suffers higher damage levels in the low forest where it occurs as a tree than in the forest where it is confined to the ground layer (Table 6.4). The amount of stem damage in November was not significantly different between the forest and the low forest for any of the species occurring at both sites with the exception of *Eucalyptus confertiflora* ($P<0.001$) which was significantly less damaged in the low forest.

Forest *Buchanania obovata* suffers distorting damage in the months immediately following post-fire emergence of 4.0% (Appendix 4). The fresh leaves of this species seem particularly attractive to gall forming Diptera or Hymenoptera (Plate 6.1). *Eucalyptus miniata* sustains similar levels of distorting damage throughout the year (Appendix 4, Table 6.1). Distorting damage on *Erythrophleum chlorostachys* in both communities peaks during the late dry season and this is attributable to the arrival of large numbers of psyllids (Appendix 4).

Tiny caterpillars cause substantial mining damage on *Acacia aulacocarpa* (Plate 6.2) and *Eucalyptus confertiflora* as indicated by the mining damage levels for these species (Table 6.1). Mining damage constitutes a substantial proportion of the high total levels of damage for the former species in the low forest and for the latter species in both communities.

Table 6.4 Median values of damage at each sampling time for the species occurring in both vegetation communities. Significant differences between communities according to the Mann-Whitney U-test are shown.

	Sample date	Total insect damage				
Species		Forest	n	Low forest	n	Significance
Buchanania obovata	Aug-87	5.1	28	0.0	31	P<0.01
	Nov-87	6.4	27	2.6	32	P<0.05
	Apr-88	9.0	27	7.1	31	NS
	Jun-88	4.1	26	6.7	33	NS
Planchonia careya	Aug-87	2.1	36	0.0	33	P<0.001
	Nov-87	3.6	40	0.0	41	P<0.001
	Apr-88	16.2	35	9.9	43	P<0.01
	Jun-88	16.5	35	7.1	38	NS
Terminalia ferdinindiana	Aug-87	0.0	21	0.0	16	NS
	Nov-87	4.1	38	5.8	28	NS
	Apr-88	4.5	34	10.3	27	P<0.01
	Jun-88	5.1	33	13.3	19	NS
Erythrophleum chlorostachys	Aug-87	0.0	19	0.0	25	P<0.01
	Nov-87	13.2	26	16.6	36	NS
	Apr-88	17.1	27	16.5	29	NS
	Jun-88	13.1	29	18.3	35	P<0.05
Eucalyptus confertiflora	Aug-87	28.2	27	5.4	33	P<0.01
	Nov-87	35.1	33	12.9	28	P<0.01
	Apr-88	35.0	26	21.2	24	P<0.05
	Jun-88	35.3	30	29.9	26	NS
Acacia aulacocarpa	Aug-87	6.3	31	0.0	35	NS
	Nov-87	7.4	35	17.4	36	P<0.001
	Apr-88	11.5	31	29.0	26	P<0.001
	Jun-88	16.7	29	42.9	21	P<0.001

There was no statistically significant relationship between height of individual stems and the individual or totalled damage classes following 1 years growth for any species in either community ($P>0.05$ in all cases). Correlations of stem damage with stem height were also non-significant ($P>0.05$).

There was no significant correlation between insect damage and the other damage category for any species at any site. Thus, it seems that

Plate 6.1 Distorting damage by galling insects on *Buchanania obovata*

Plate 6.2 Mining damage to *Acacia aulacocarpa*.

insect damage is not a cause of general senescence. General senescence becomes prominent towards the end of the wet season and increases for the rest of the post-emergence year for both deciduous and evergreen species and represents the deterioration of old leaves following a period without growth (Fig. 6.2). Stem death is common during the latter half of the post-emergence year and is a reflection of general senescence. Stem death was not recorded as other damage by this method and consequently this damage class is an underestimate of general senescence. Not surprisingly general senescence is greatest for the deciduous species *Terminalia ferdinandiana* (Table 6.1). The extent of senescence is surprisingly low for the semi-deciduous species *Eucalyptus confertiflora* (Table 6.1) indicating that this species becomes more deciduous with the switch from woody sprout to tree lifeforms.

6.3.2 Insecticide experiment

Phytotoxic insecticide effects can be determined by comparing the other damage category between the insecticide treatment and the control. This effect was statistically significant ($P<0.001$) for *Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus confertiflora* and *Acacia aulacocarpa*. Insecticide significantly protected *Terminalia ferdinandiana, Erythrophleum chlorostachys, Eucalyptus confertiflora, Acacia aulacocarpa* and *Eucalyptus tetrodonta* from insect damage. The difference in total damage between sprayed and unsprayed treatments was significant only for *Acacia aulacocarpa* and *Eucalyptus tetrodonta* ($P<0.001$). The difference in mean total damage between the sprayed and control plots, 4 months after emergence, was 2.9 and 9.5% for *Eucalyptus tetrodonta*, and 1.8 and 8.1% for *Acacia aulacocarpa* respectively. *Buchanania obovata* and *Planchonia careya* were neither significantly protected from insects nor adversely affected by spraying ($P>0.05$).

The species that were not protected by insecticide showed no significant growth response ($P>0.05$). Furthermore, there was no significant difference in heights between the water treatment and the control ($P>0.05$). Thus, it seems the amount of water used during spraying was insufficient to enhance growth. For *Acacia aulacocarpa* there was no significant difference in growth between any combinations of

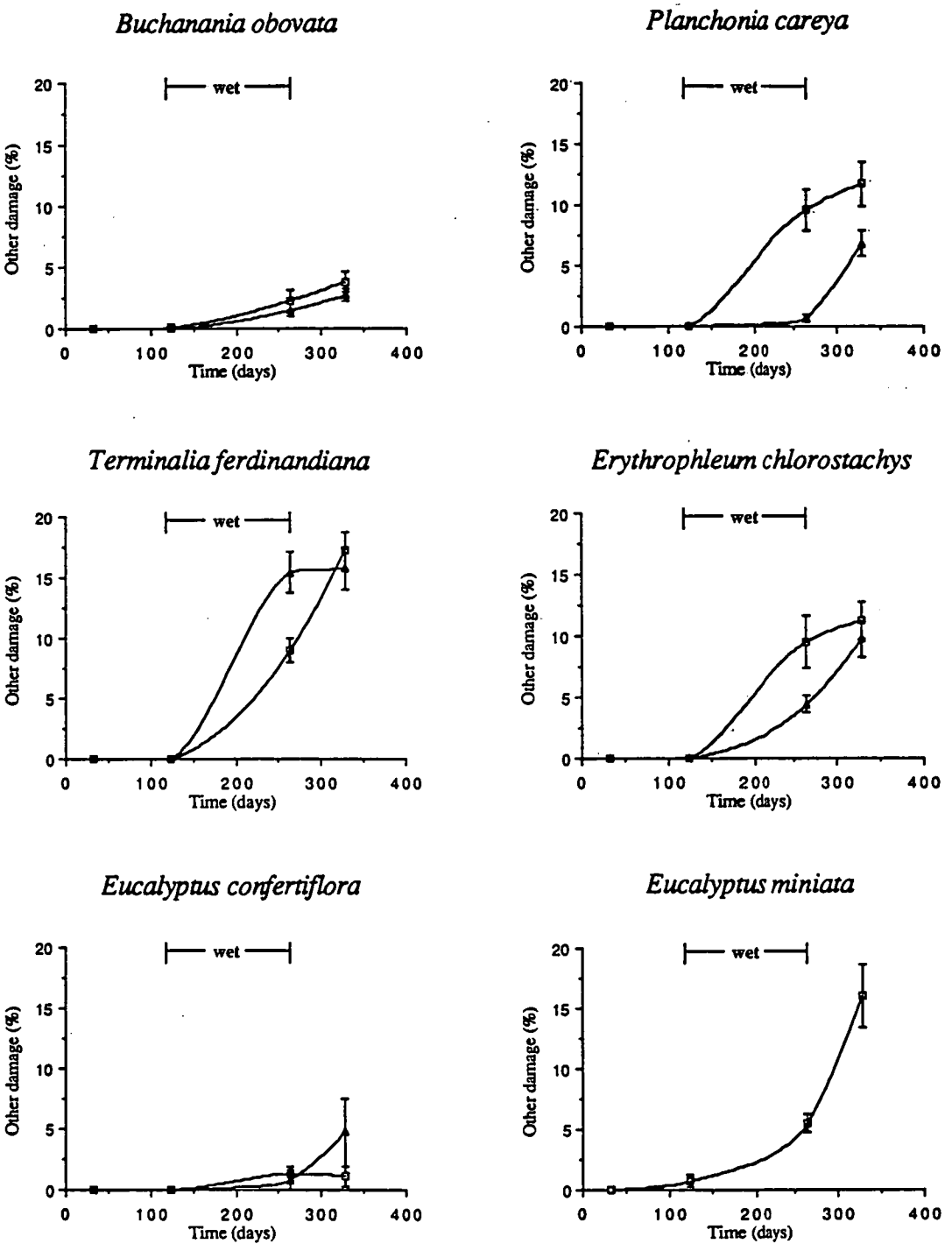


Figure 6.2 Mean (and s.e.m.) Other damage, in terms of the damage condition of the plant and rate of leaf decay for eight tree species in two vegetation types (□ forest, ▲ low forest). The wet season period is indicated.

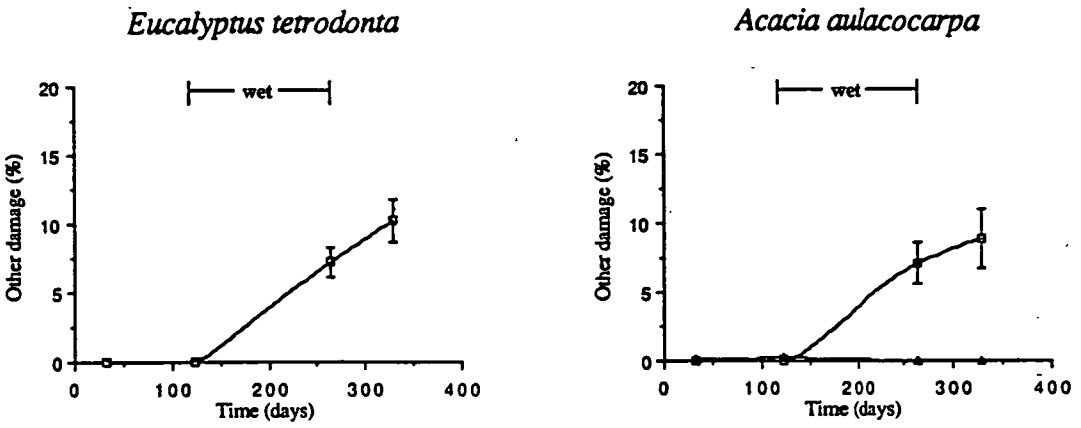


Figure 6.2 continued

---

insecticide sprayed, water sprayed or control treatments ($P>0.05$). *Eucalyptus tetrodonta* showed a significant increase in growth ($P<0.01$) in the insecticide treatment compared to the watered treatment. However, the individuals in the control plot were also significantly taller than the watered plot ($P<0.05$) and there was no significant difference for *Eucalyptus tetrodonta* ($P>0.05$) between sprayed and control plots. It seems that the significance of any differences do not represent growth response from insect protection. Differences in height could not be discerned by the appearance of the plants.

6.3.3 Phytophagous insect community

Appendix 5 lists the collection by sample according to taxa. The total insect collection consisted of 3531 individuals- 34.9% Psylloidea (14 species), 40.6% Other Hemiptera (128 species), 13.9% Orthoptera (65 species) and 10.6% Coleoptera (62 species). Phasmatodea was the only other insect order represented, and this group was only a miniscule proportion of the total collection. A further 147 Lepidoptera larvae were counted. There were only very occasional miscellaneous larvae

and there presence was not recorded. Larval Diptera and Hymenoptera were sometimes conspicuous by the presence of galls (Section 6.3.1).

Fig. 6.3 presents the abundance of the major insect groups according to season, plant host and vegetation type. Table 6.5 provides the statistical significance of these results. The seasonal abundance of insect groups for all plant hosts combined are presented for each vegetation type in Fig. 6.4.

Orthoptera were the only major insect group that showed significant variation ($P<0.05$) between the disjunct wet season samples from the same forest community at the main study site and at Milikapiti. The ANOVA results were inconclusive regarding differences in the abundance of insects between the forest and the low forest. There were indications of greater abundance of Other Hemiptera, Orthoptera and total chewing insects in the low forest compared to the forest (Table 6.5 and Fig. 6.4). However, these apparent differences may be a product of their abundance on a few plant species and the unbalanced nature of the experiment. The abundance of these groups was especially low on *Eucalyptus miniata* and *Eucalyptus tetrodonta* that are confined to the forest (Fig. 6.3). When these species are excluded from the analysis the effect of plant community on the abundance of Other Hemiptera, Orthoptera and total chewing insects is non-significant ($P>0.05$, Table 6.5).

Psyllid and caterpillar abundance is affected by the interactive influence of host species, community and season. Psyllids were particularly abundant during the late dry season, presumably because of flowing sap in the active post-fire stages of regrowth. This group was particularly conspicuous on *Erythrophleum chlorostachys* and *Eucalyptus miniata*. Lerps provided evidence of psyllids on other tree species although the insects were not seen during the sampling period because of their short lifecycle. Caterpillars were most prevalent during the dry season (Fig. 6.4) although for individual plant hosts their numbers can peak during the early or late parts of this season (Fig. 6.3). A dry season peak in caterpillar abundance is not evident for *Eucalyptus confertiflora* (Fig. 6.3). Caterpillars were more prominent on *Planchonia careya, Eucalyptus confertiflora* and *Acacia aulacocarpa*

Figure 6.3 Seasonal abundance distribution of the major phytophagous insect groups according to their host species and vegetation community. M- Missing sample. LD- Late dry season; W- Wet Season; ED- Early dry season.

Buchanania obovata

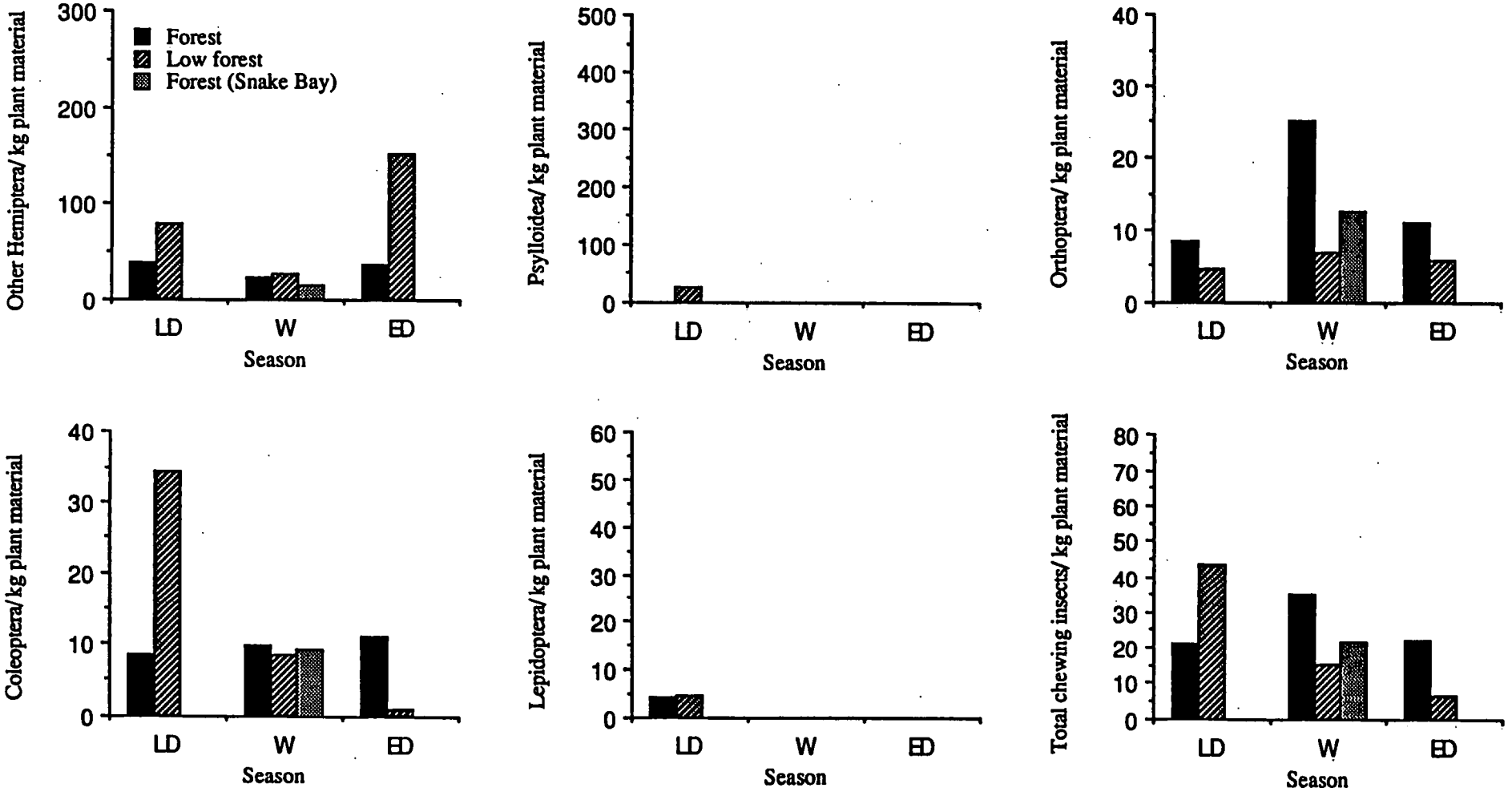


Figure 6.3 continued

Planchonia careya

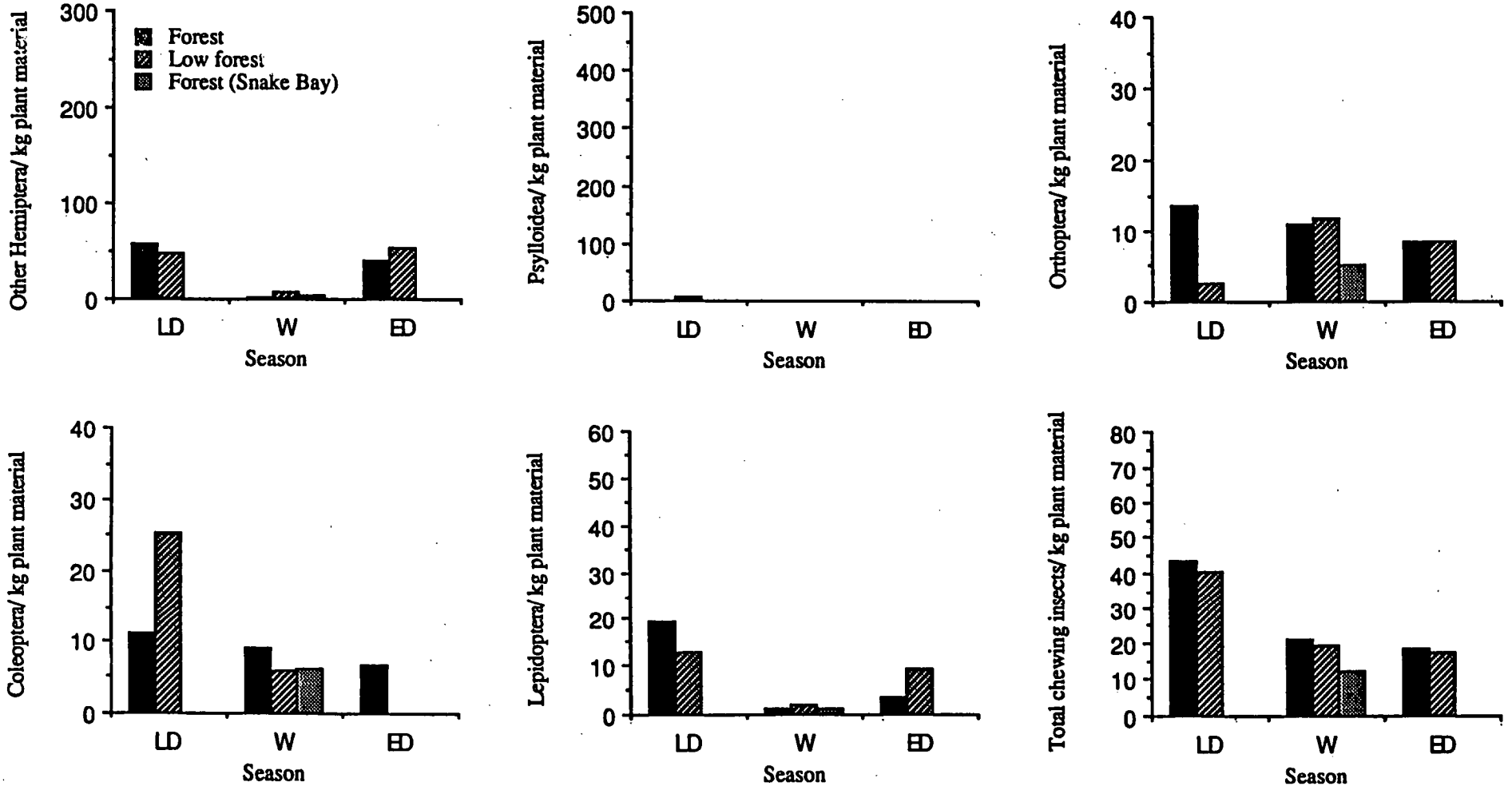


Figure 6.3 continued

Terminalia ferdinandiana

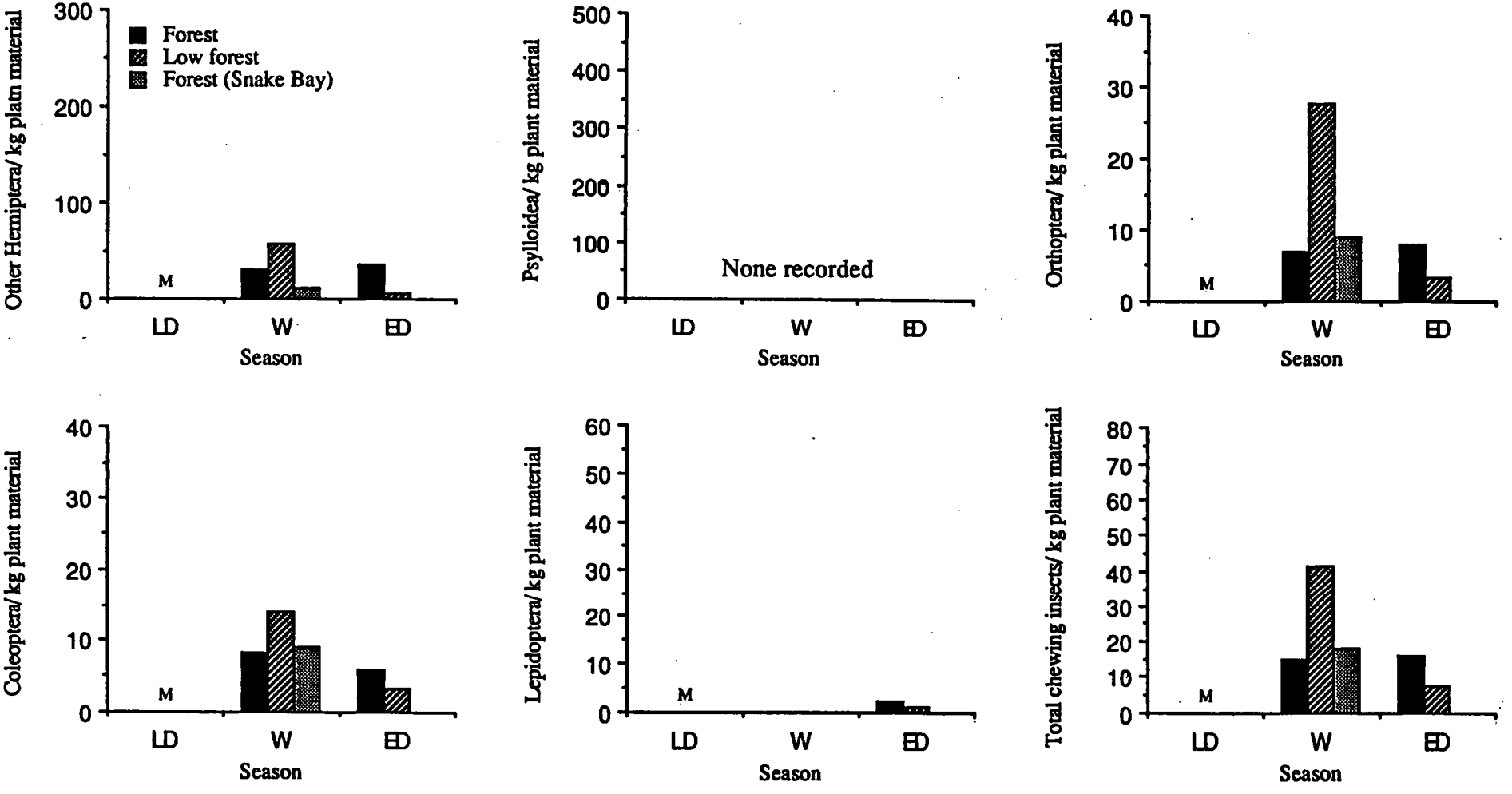


Figure 6.3 continued

Erythrophleum chlorostachys

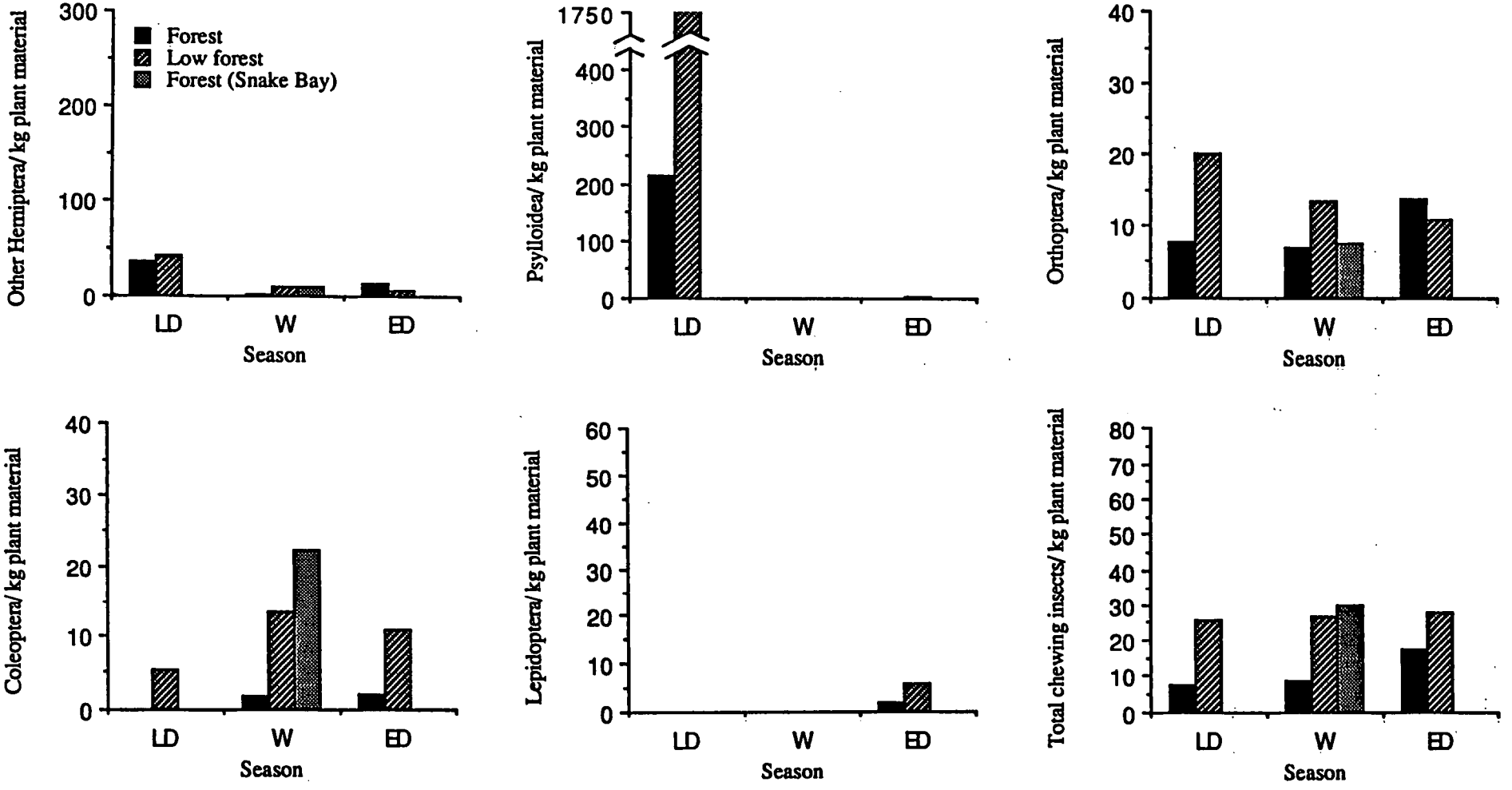


Figure 6.3 continued

Eucalyptus confertiflora

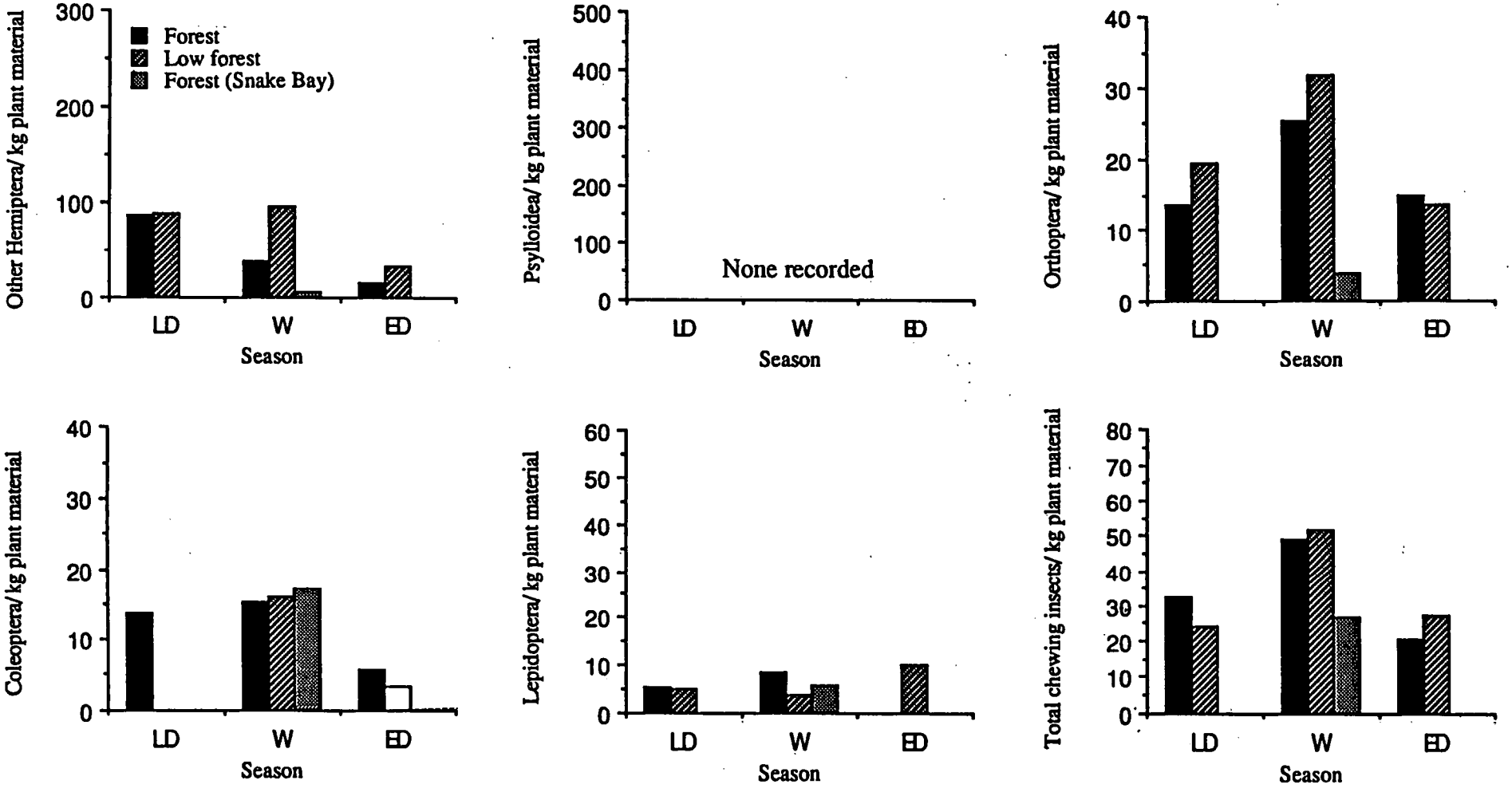


Figure 6.3 continued

Eucalyptus miniata

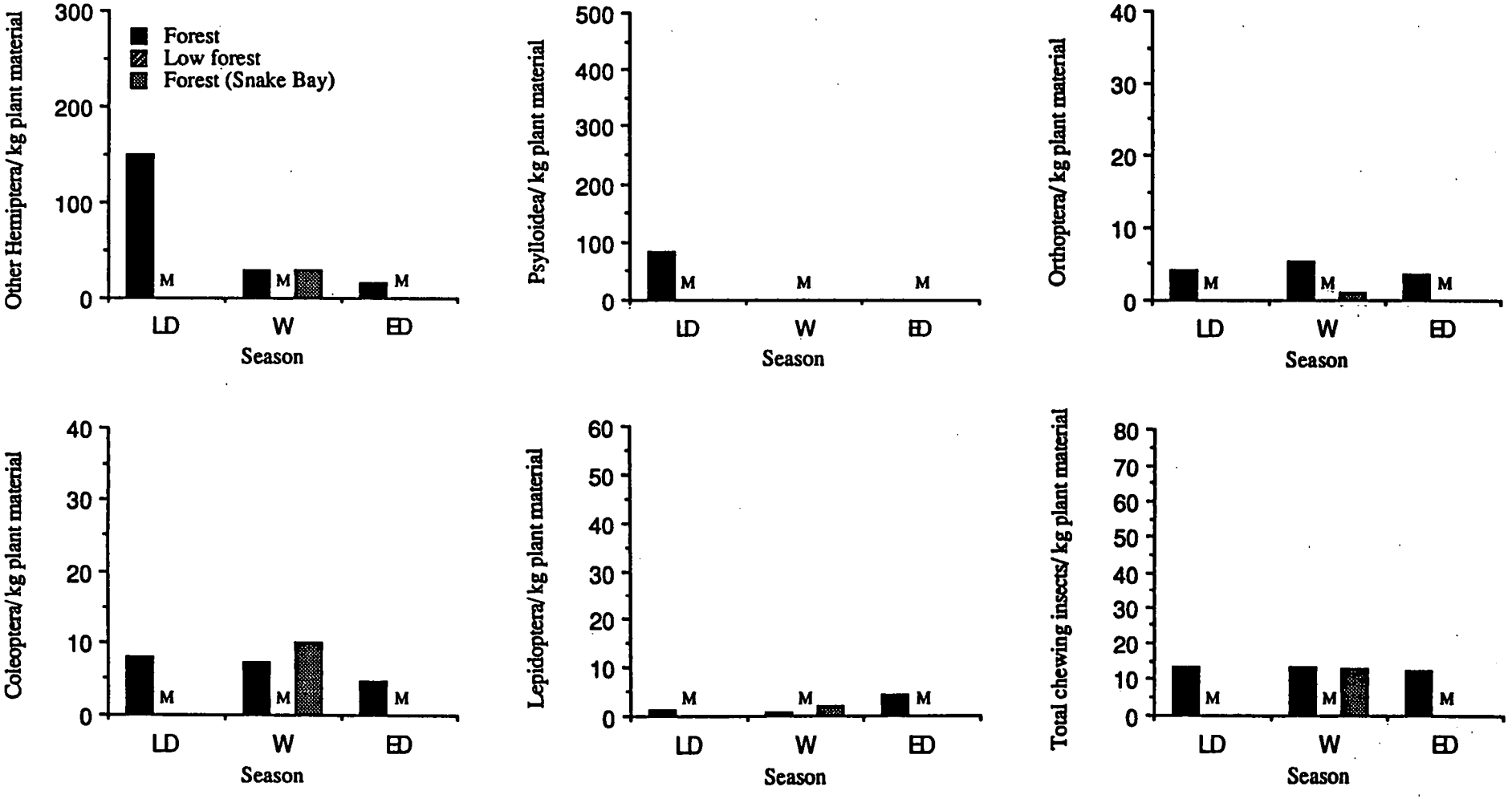


Figure 6.3 continued

Eucalyptus tetrodonta

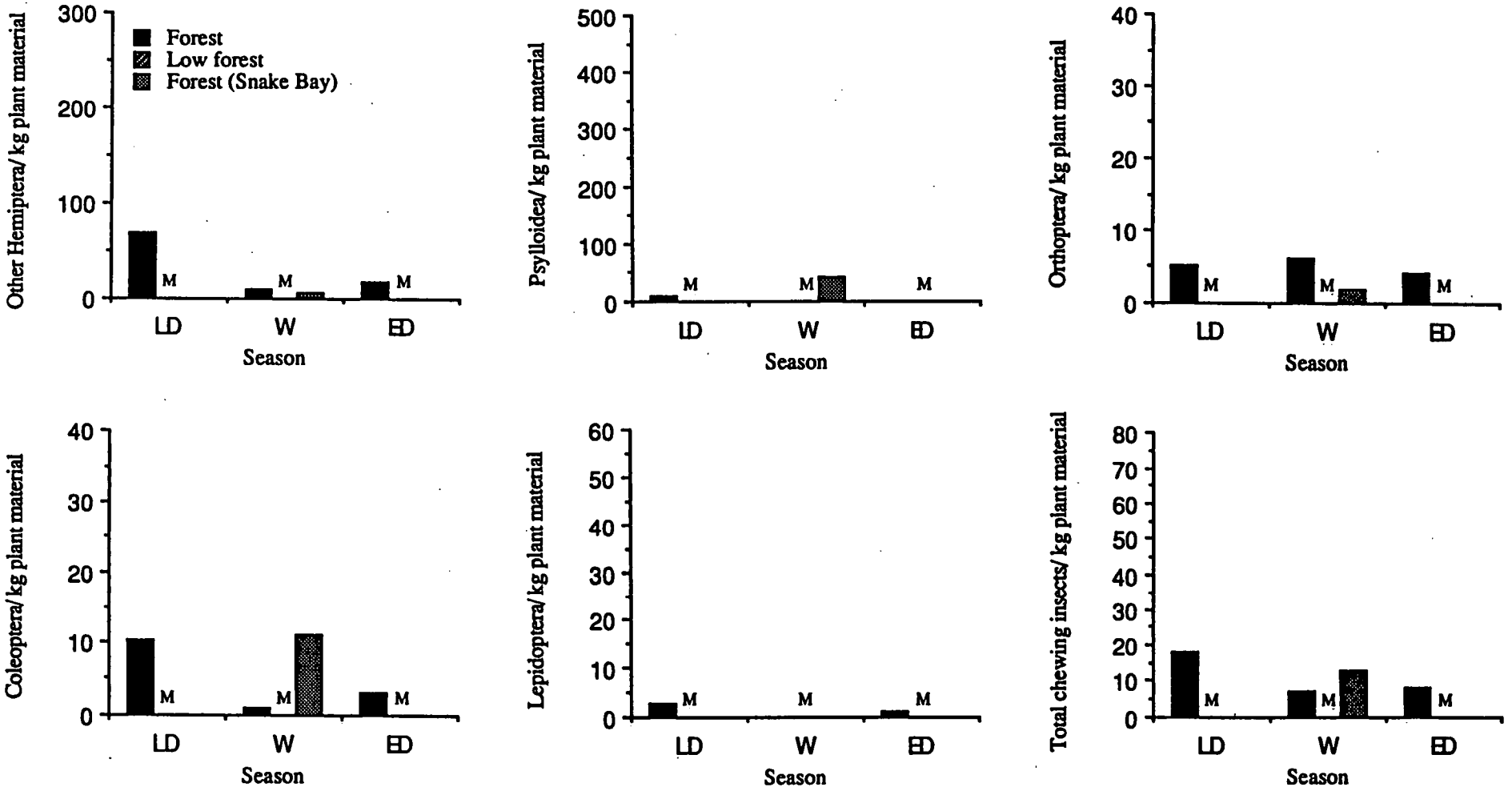


Figure 6.3 continued

Acacia aulacocarpa

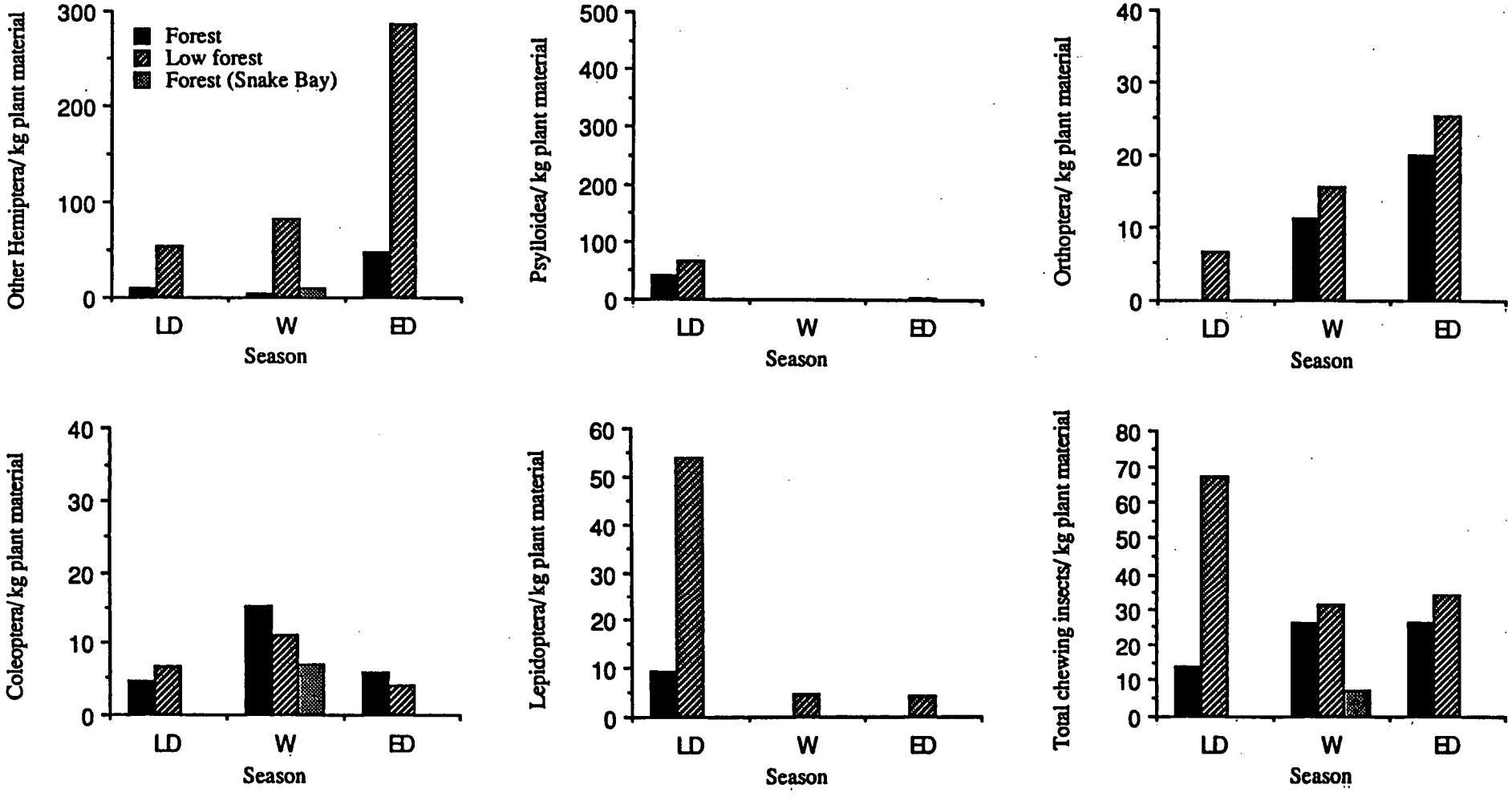


Table 6.5 Significance values for three analyses of variance of the major phytophagous insect groups according to host plant lifeform, host plant species, plant community and season.

	Other Hemiptera	Psylloidea	Orthoptera	Coleoptera	Lepidoptera	Total chewing insects
Threeway ANOVA						
Plant community		NS	*	NS	*	*
Season		***	NS	NS	**	NS
Plant host lifeform		NS		NS	NS	NS
Community x Season	NS	NS	NS	NS	NS	NS
Community x Lifeform	**	NS	*	NS	NS	NS
Season x Lifeform	**	NS	NS	NS	NS	NS
Community x Season x Lifeform	NS	NS	NS	*	NS	NS
Twoway ANOVA						
Plant community	*	NS	*	NS	NS	**
Season	**	***	NS	*	**	NS
Community x Season	NS	NS	NS	NS	NS	NS
Oneway ANOVA						
Plant host species	NS	NS	NS	NS	NS	NS

* P<0.05, ** P<0.01, *** P<0.001. Main effects are excluded if an interactive effect exceeds P<0.01

Table 6.5 continued

Threeway ANOVA with incomplete species samples removed

	Other Hemiptera	Psylloidea	Orthoptera	Coleoptera	Lepidoptera	Total chewing insects
Plant community	**		NS	NS		NS
Season	**		NS	NS		NS
Plant host species	*		NS	NS		NS
Community x Season	NS		NS	NS		NS
Community x Species	*	NS	NS	NS		NS
Season x Species	*		NS	NS		NS
Community x Season x Species	NS	***	NS	NS	**	NS

* P<0.05, ** P<0.01, *** P<0.001. Main effects are excluded if an interactive effect exceeds P<0.01

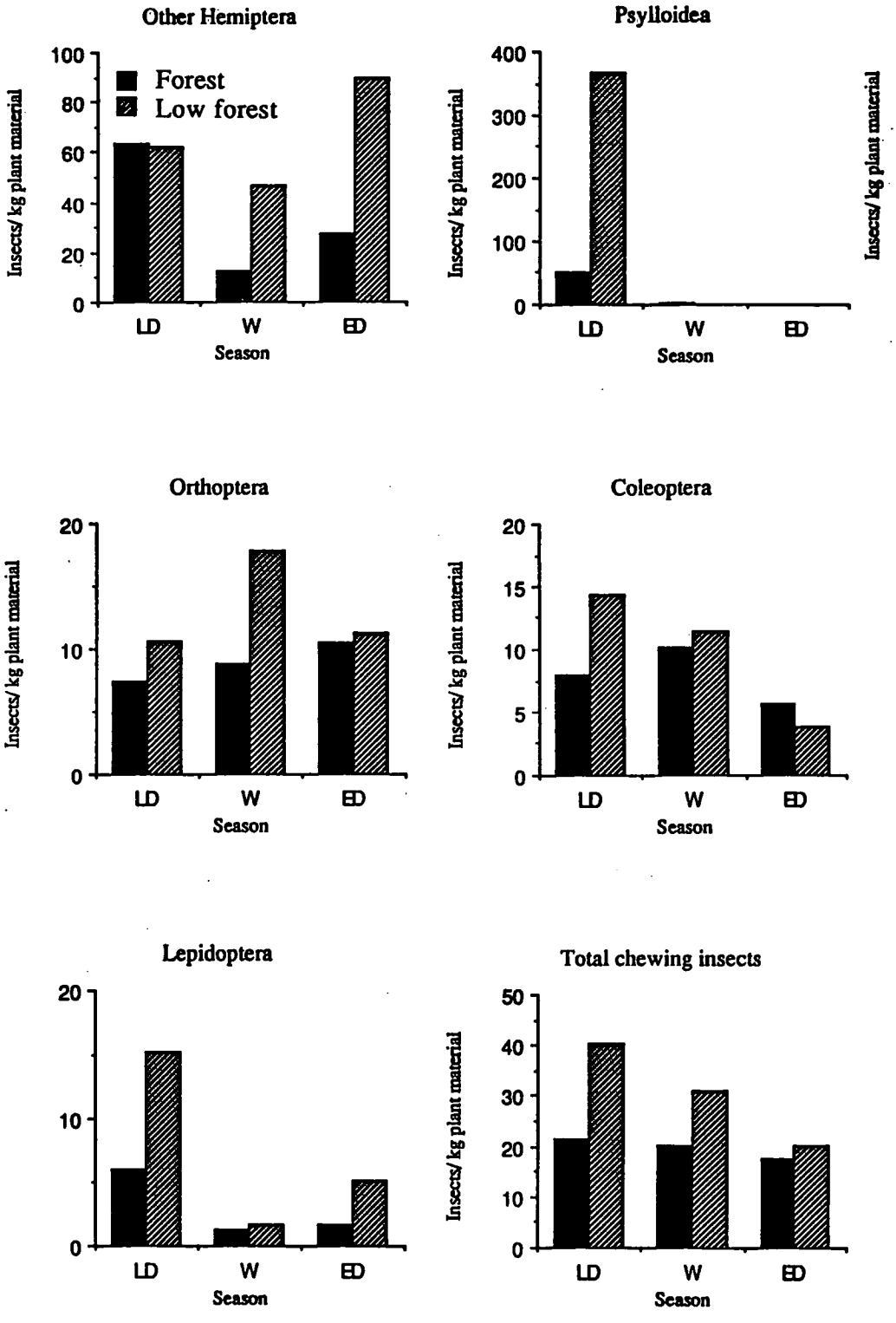


Figure 6.4 Mean seasonal abundance distribution of the major phytophagous insect groups in the two plant community for all plant host species combined. LD- late dry season; W- Wet season; ED- Early dry season.

than the other species and were particularly obvious on the latter species in the low forest. Other Hemiptera were also more evident during the dry season (Fig. 6.4) although this relationship is not evident for *Terminalia ferdinandiana* and *Eucalyptus confertiflora* (Fig. 6.3).

Twenty-one species of bugs, seven species of Orthoptera and six species of beetles occurred nine or more times. Nine bug species, one Orthoptera and one species of beetle showed some significant relation with their host plant species (Table 6.6). However, ANOVA is insensitive to large numbers of individuals on a single plant host and there were other insects that seemed to have strong alliance with particular hosts. More than 80% of the individuals of four Other Hemiptera (Achilidae sp. no. 63, Cicadellidae sp. no. 66, Membracidae sp. no. 95, Pseudococcidea sp. no. 156) and three of the four frequent psyllids (Psylloidea sp. no. 124 ,125, 126) occurred on a single host species (Table 6.6). Three Other Hemiptera (Cicadellidae spp. nos. 14, 16, 34) were confined to the genera *Eucalyptus* or *Acacia*, one mealy bug (Pseudococcidea sp. no. 155) was confined to the eucalypt subgenera *Eudesmia* and another bug (Achilidae sp. no. 63) was found only on the broadleaved species *Buchanania obovata, Planchonia careya* and *Terminalia ferdinandiana* (Table 6.6).

The only frequent insect species confined to a particular community were found in abundance on one individual host plant. It is difficult to draw conclusions about the seasonality of individual species because sampling was restricted to three discrete sample times which may have coincided with the hatching of species with short lifecycles. However, ANOVA revealed that seasonal preference seemed to be most common with the Orthoptera (with six of the seven species responding to this factor at the $P<0.01$ level). One bug (Ricaniidae sp. no. 98, $P<0.001$) was most prominent during the dry season samples while another bug (Tropiduchidae sp. no. 18, $P<0.01$) and two orthopterans (Stenopelmatidae sp. no. 60, $P<0.01$; Gryllidae sp. no. 8, $P<0.001$) were most abundant during the early dry season. Another orthopteran species was favoured during the late dry season sample (Gryllidae sp. no. 45, $P<0.001$). Two members of the Orthoptera (*Goniaea* sp. no. 15,

Table 6.6 Percentage occurrence by plant host species of the insect species occurring as nine or more individuals. Significant ANOVA results are presented.

Hemiptera	*Buchanania obovata*	*Planchonia careya*	*Terminalia ferdinandiana*	*Erythrophleum chlorostachys*	*Eucalyptus tetrodonta*	*Eucalyptus miniata*	*Eucalyptus confertiflora*	*Acacia aulacocarpa*	n	no. of samples
Achilidae No. 63*	10.1	5.1	84.8	-	-	-	-	-	25	10
Delphacidae No. 11	9.4	4.7	11.8	16.0	14.8	26.3	13.2	3.8	84	67
Dictyopharidae No. 8*	5.9	8.7	53.3	14.6	-	-	14.6	2.9	29	16
Flatidae No. 21*	0.9	14.4	-	0.9	6.3	73.9	1.8	1.8	73	28
Flatidae No. 48	5.1	20.2	35.4	5.1	-	8.9	15.1	10.2	17	15
Fulgoridae No. 3	20.9	38.3	1.2	14.8	1.5	7.5	15.7	-	110	64
Ricaniidae No. 98	10.6	46.3	24.0	6.6	-	4.6	7.9	-	69	44
Tropiduchidae No. 7*	2.6	23.3	58.0	2.6	13.6	-	-	-	30	17
Tropiduchidae No. 78	9.4	56.4	4.3	3.1	-	11.0	6.3	9.4	30	21
*Cicadella pathaon**	13.7	8.8	2.8	2.0	17.1	36.0	18.7	1.0	78	42
Cicadellidae No. 14	-	-	-	-	15.8	28.4	55.9	-	45	26
Cicadellidae No. 15*	-	-	-	-	31.3	62.7	-	-	20	18
Cicadellidae No. 34*	-	-	-	-	20.4	67.9	9.7	1.9	32	24
Cicadellidae No. 66	100.0	-	-	-	-	-	-	-	192	4
Membracidae No. 95	-	-	-	-	-	4.8	-	95.2	36	5
Pseudococcidae No. 157*	-	-	-	-	21.2	78.8	-	0.0	85	35
Pseudococcidae No. 156	-	-	-	1.3	-	-	-	98.7	157	9
Psylloidea No. 132	-	-	-	1.3	98.7	-	-	-	45	3
Psylloidea No. 124	-	-	-	100.0	0.0	-	-	-	363	8
Psylloidea No. 131	3.4	13.7	4.8	34.3	6.0	24.0	3.4	10.3	25	10
Psylloidea No. 126	-	-	-	-	-	100.0	-	-	58	5

* Species significantly associated with host species ($P<0.01$)

Collecting numbers refer to specimens held at the CSIRO Tropical Ecosystems Research Centre, Darwin.

Table 6.6 continued

	Buchanania obovata	*Planchonia careya*	*Terminalia ferdinandiana*	*Erythrophleum chlorostachys*	*Eucalyptus tetrodonta*	*Eucalyptus miniata*	*Eucalyptus confertiflora*	*Acacia aulacocarpa*	n	no. of samples
Orthoptera										
Goniaea sp. No. 15	6.3	-	-	6.3	10.9	32.8	43.7	-	13	11
Eumastacidae No. 2*	10.1	2.2	6.3	40.4	3.9	15.7	9.0	12.4	80	47
Gryllidae No. 45	17.4	13.9	0.0	17.4	24.3	6.1	20.9	-	25	11
Gryllidae No. 36	0.0	18.5	25.9	6.2	10.8	32.4	6.2	-	12	7
Gryllidae No. 8	50.7	14.5	20.3	-	-	-	7.3	7.3	13	9
Stenopelmatidae No. 60	33.3	44.4	-	11.1	-	-	11.1	-	9	6
Tettigoniidae No. 23	5.6	22.4	23.4	7.0	7.4	4.9	16.7	12.6	63	44
Coleoptera										
Apionidae No. 11	-	9.2	-	73.8	-	10.8	3.1	3.1	32	12
Chrysomelinae No. 6	-	16.7	-	-	14.6	43.8	25.0	-	10	10
Eumolpinae No. 8	34.5	6.9	-	20.7	24.1	-	13.8	-	13	10
Eumolpinae No. 7	-	34.6	24.2	8.7	-	15.2	8.7	8.7	10	9
Otiorrhynchinae No. 9	3.1	12.4	8.6	3.1	16.2	37.9	15.4	3.1	24	18
Otiorrhynchinae No. 10*	3.9	1.0	12.3	2.9	20.5	40.9	14.6	3.9	72	39

* Species significantly associated with host species ($P<0.01$)
Collecting numbers refer to specimens held at the CSIRO Tropical Ecosystems Research Centre, Darwin.

P<0.001; Tettigoniidae sp. no. 23, P<0.001) and one beetle (Otiorrhynchinae sp. no. 10, P<0.01) had pronounced abundance peaks during the wet season.

A comparison of all the sweep samples between day and night revealed no significant diurnal fluctuations in total insect abundance (mean values for insect numbers from twenty sweeps were 6.5 during the day and 6.9 at night). However, the Orthoptera were significantly more abundant during the night (P<0.001; mean values 1.5 and 3.3 per sweep sample). It is common knowledge that members of the orthopteran superfamilies Gryllacridoidea and Grylloidea, that were frequently represented in these samples (Appendix 5), have nocturnal tendencies (CSIRO 1970).

6.4 Discussion

6.4.1 Comparison with other studies

Table 6.7 summarises the measurements of insect damage from native Australian vegetation. These studies are not entirely comparable. Some investigators used discrete measurement of damage and others used longterm monitoring techniques. Lowman (1984) found large discrepancies between these alternative techniques, for some rainforest tree species. However, longterm and discrete sampling was compared here and there were only slight differences. The longterm/discrete ratio was less than 1.01 for all species at both sites. This reinforces the findings of Landsberg (1989) who found little difference between these techniques for damage assessment of *Eucalyptus blakelyi* leaves. Other idiosyncrasies of this study need to be noted before it is considered in the context of other studies. Most insect damage assessments have only determined leaf area missing. The present study and the work of Landsberg and Wylie (1987) allowed for damage by distorting insects. This type of herbivory accounts for a minor portion of total damage in both these studies.

Yen (1989) showed that coppice regrowth suffers more than canopy foliage. It has been demonstrated herein that the suppressed stems have a peculiar growth strategy whereby they have been dormant for

five months at the time of the June sampling. Consequently insect attrition is not compensated by new growth as it might be in a forest canopy. These peculiarities suggest that the results presented here were maximal values for this forest. Damage levels for all measured species in the ground layer of the tropical forest ranged from 7.8-43.2%. Damage levels for the forest dominants *Eucalyptus miniata* and *Eucalyptus tetrodonta* were 18.4 and 14.7% respectively. Given the fact that several features of this study suggest that damage estimates will be maximum values for this forest these values do not seem abnormally high compared to levels reported for the dominant trees in other Australian forests (Table 6.7).

While this study examined the dynamics only of phytophagous insects some comparison can be made with more comprehensive studies of the invertebrate communities of southeastern Australia (subalpine eucalypt canopies: Ohmart *et al.* 1983b, regional: Woinarski and Cullen 1984, mallee vegetation: Yen 1989). The following features of the insect community on Melville Island (Fig. 6.5) seem to contrast with the fauna of eucalypt vegetation in southeastern Australia:

1) Non-psyllid Hemiptera were particularly frequent in the ground layer of the tropical eucalypt forest.
2) The Orthoptera represent 9.38% of the total phytophagous insect community sampled on Melville Island. This proportion is relatively high and their prevalence in the tropical eucalypt forest has been suggested previously (Andersen and Lonsdale 1990). Sampling strategies that allow the most agile insects to escape, may be a partial explanation for the bare representation of the Orthoptera in southeastern Australian vegetation.
3) Caterpillars were relatively less abundant than in the tree canopies studied by Ohmart *et al.* (1983b). This group is not distinguished in the other Australian studies.
4) Thysanoptera were minor components of the southern folivorous insect community but were not encountered during this study.

Direct comparison with Morrow's (1977b) examination of host specificity is difficult because she sampled from only three host species and included locally infrequent insect species in her estimates.

Table 6.7 Review of quantified studies of insect herbivory in native Australian vegetation

Author/s	Location	Vegetation type	Plant species	Lifeform	Sampling method	Damage level (%)
Burdon & Chilvers (1974a)	Brindabella Ranges, ACT	Sub-alpine eucalypt forest	*Eucalyptus dalrympleana, E. delegatensis, E. dives, E. pauciflora, E. radiata, E. viminalis*	Mature tree	Discrete sample, with some account of missing leaves	2.7-27.5
Burdon & Chilvers (1974b)	Brindabella Ranges, ACT	Sub-alpine eucalypt forest	*Eucalyptus dalrympleana, E. pauciflora*	Mature tree	Discrete sample, with some account of missing leaves	8-33
Kile (1974)	Dover, Tas	Eucalypt forest	*Eucalyptus globulus, E. obliqua, E. regnans*	Mature tree	Discrete sample	6-40
Journet (1981)	near Canberra, ACT	Eucalypt woodland	*Eucalyptus blakelyi*	Mature tree	Discrete sample	15-52.5
Fox & Morrow (1983)	southern Australia	Sub-alpine eucalypt, eucalypt forest, lowland woodland & mallee	44 *Eucalyptus* species	Coppice regrowth to mature tree	Discrete sample	5-44
Landsberg & Wylie (1983)	near Brisbane, Qld	Eucalypt forest & farmland	*Eucalyptus acmenoides, E. maculata, E. propinqua, E. tereticornis, E. tessellaris*	Mature tree	Discrete sample	6-30
Ohmart *et al.* (1983a)	Brindabella Ranges, ACT	Sub-alpine eucalypt forest	*Eucalyptus delegatensis, E. dives, E. pauciflora*	Mature trees	Discrete sample	2-15

Table 6.7 continued

Author/s	Location	Vegetation type	Plant species	Lifeform	Sampling method	Damage level (%)
Lowman (1985)	NSW, SE Qld	Sub-tropical, warm-temperate, cool-temperate rainforest	*Nothofagus moorei*, *Doryphora sassafras*, *Ceratopetalum apetalum*, *Dendrocnide excelsa*, *Toona australis*,	Mature tree (lower - upper canopy)	Longterm monitoring	1.8-53.8
Lowman & Heatwole (1987)	New England, NSW	Eucalypt woodland	*Angophora floribunda*, *Eucalyptus blakelyi*, *E. caliginosa*, *E. melliodora*, *E. viminalis*	Saplings	Longterm monitoring	7.6-27.6
Lowman *et al.* (1987)	Walcha, NSW	Farmland	*Eucalyptus nova-anglica*	Mature tree	Discrete sample	9.2-11.3
Robertson & Duke (1987)	near Townsville, Qld	Mangrove	25 Mangrove species	Mature tree	Discrete sample	0.3-35.0
Yen (1989)	Big Desert, Vic	Eucalypt mallee	*Eucalyptus dumosa*, *E. foecunda*, *E. incrassata*	Coppice regrowth & mature trees	Discrete sample	8.4-20.8
Landsberg (1989, 1990)	Hall, ACT	Farmland	*Eucalyptus blakelyi*	Mature trees	Longterm monitoring	3.6-25.1
Williams (1990)	Brindabella Ranges, ACT	Sub-alpine eucalypt forest	*Eucalyptus delegatensis*, *E. dives*, *E. pauciflora*	Coppice regrowth	Discrete sample	7.4-20.7
Present study	Melville Island, NT	Eucalypt forest	*Acacia aulacocarpa*, *Buchanania obovata*, *Erythrophleum chlorostachys*, *Eucalyptus confertiflora*, *E. miniata*, *E. tetrodonta*, *Planchonia careya*, *Terminalia ferdinandiana*	Coppice regrowth	Longterm monitoring	7.8-43.2

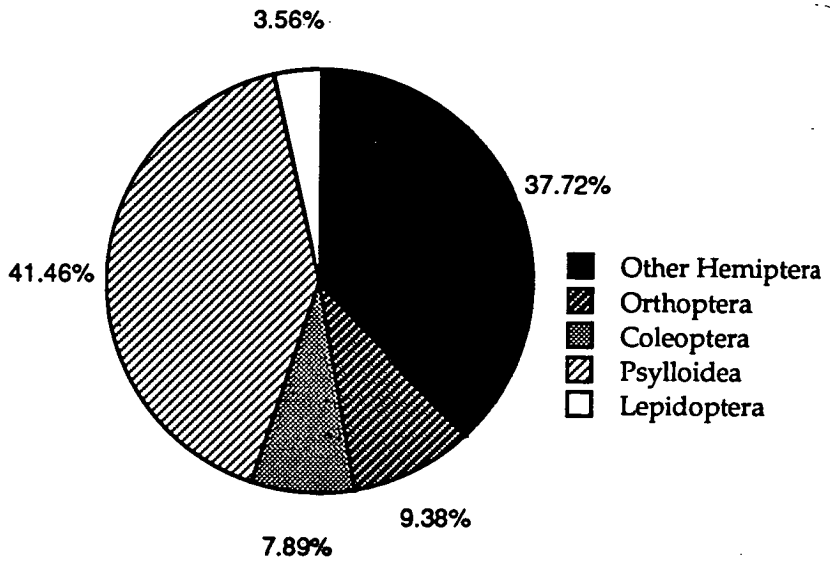


Figure 6.5 The proportions of the major phytophagous insect groups from foliage of woody sprouts in the ground layer of the eucalypt forest on Melville Island.

However, the raw data included in her work allows calculation of a more rigorous estimate following the exclusion of species occurring as less than nine individuals. This reduces Morrow's data set from 80 to 48 species. Morrow's system of defining a specialist (80% or more of its individuals collected from one host) suggests that phytophagous insects in the ground layer of northern Australian eucalypt forest are more generalist than in the canopies of southern Australia. Sixty-three percent were specialists in Morrow's study compared to only 21% in this study.

6.4.2 Insect effects on vegetation

The insect community was only sampled at three times. However, more continuous sampling from elsewhere in the tropics (Bigger 1976, Wolda 1980, Gillon Y. 1983) and the knowledge that insect outbreaks are relatively rare in natural systems (Strong *et al.* 1984 p 136) suggests that fluctuations are relatively smooth. On this basis the sampling technique employed here should be indicative of seasonal patterns. The relative destructive effects of different insect groups probably

accounts for disparities between damage and insect abundance (c.f. Figs. 6.1 and 6.3). In general large insects must consume more plant material than small insects. Relative to the other insects collected in this study, Orthoptera must consume a disproportionate share of plant material to support their relatively large body size. The prevalence of this group at night indicates that large quantities of leaf material are consumed after the sun is down. On this basis the effects of chewing insects on vegetation is better assessed by the damage plants have incurred rather than by the abundance of the insects.

This study provides the opportunity to assess the potential influence of phytophagous insects on the regeneration process in the tropical eucalypt forest. The insecticide experiment contributed to the resolution of this issue but was hampered by unforeseen problems. The chemicals employed had phytotoxic effects and it is suggested that future work should employ chemicals that have repellant rather than insecticidal properties. Surface acting chemicals tend to be less phytotoxic. Furthermore, repellants may be more appropriate because in the small island that is the experimental plot it is rather pointless to kill insects, after they have consumed enough plant material for a lethal dose, when they will be promptly replaced by mobile insects from the unpoisoned surrounds. Presumably repellants only have to render plants slightly less attractive to divert insects to the surrounding area of more palatable plant material.

Despite limitations the insecticide treatment was successful in reducing insect damage to about a quarter of its usual levels for two tree species. Neither of these species showed a growth response. This result contrasts with another Australian study that clearly shows positive growth response of eucalypt saplings following protection using insecticide (Lowman and Heatwole 1987). Furthermore, there was no evidence from the damage monitoring plots that the tallest stems were those that had suffered the least damage.

There was no evidence that tree species suffered less insect attack in the community where they were most successful compared to the community where that tree species was confined to the ground layer. The structure of the insect community reflects this result.

Erythrophleum chlorostachys and *Terminalia ferdinandiana* have more total chewing insects associated with them in the low forest than the forest (Fig. 5.3) but both these species are more prevalent as trees in the former community.

If fire is excluded from the tropical eucalypt forest many stems of woody sprouts, particularly the evergreen species, die back to ground level (Chapter 3). There is no evidence that this phenomenon is precipitated by herbivory. It was evident from this study that the leaf age of savanna trees is about 7 months. Because stems produce few new leaves during a long dormant period the dieback of these stems may be attributable to the lack of photosynthates following leaf abscission.

If growth cessation during the wet season is an artefact of an adaptation to avoid periods of intense herbivory increases in damage and phytophagous insect abundance during this period might be expected. Such patterns are clearly not evident from this study. The various estimates of phytophagous insect activity used here show no clear seasonal trends. However, it is evident that the wet season is not a period of intense phytophagy. This result is difficult to interpret because the cessation of growth may represent an evolutionary response to previous insect levels. The absence of young leaves may in turn have initiated declines in insect abundance. However, if such a mechanism has occurred the resulting patterns contrast starkly with evidence from elsewhere in the seasonal tropics.

Studies in a range of rainforest types on Australia's eastern seaboard (Lowman 1982, Frith and Frith 1985) show that insect abundance is intimately linked with the growth response of plants to seasonal fluctuation. In these rainforests where the climate is seasonal this means that insects are more abundant during the wet period. This phenomenon has been recorded from other continents with seasonally tropical climates (Bigger 1976, Wolda 1989 and references therein), including tropical savanna (Gillon Y. 1983). Janzen and Schoener (1968) and Janzen (1973) found that as the climate became less seasonal insect abundance fluctuated less. It needs to be emphasized that the samples in this study were from the leaves of stunted trees rather than generalized samples as might be obtained by sweep netting the ground

layer. Presumably generalized wet season samples from the tropical eucalypt forest would collect greater numbers of insects because this is the only period when there is live herbage. Nevertheless, the results are in stark contrast to the data collected from tropical tree foliage.

Homoptera were more abundant during the dry season in our samples and this seasonal trend is the reverse of that found by Wolda (1978). Yen (1989) suggests that the more active growth of coppice regrowth compared to tree canopy foliage favours the feeding requirements of sucking insects. This probably explains the psyllid swarms during the early part of the regrowth period. It is more difficult to understand the increase in abundance of Other Hemiptera during the early dry season, after depressed abundances in the wet season, despite the cessation of growth during this period. This result clearly contradicts studies from other continents that correlate the abundance of sucking insects with the availability of sap (see references in Hodkinson and Casson 1987). It is possible that sap flow has resumed with the onset of the dry season but photosynthates are translocated to the root system rather than foliar meristems. If sucking insects have important detrimental effects there is no evidence of plants avoiding growth during periods of intense bug activity. It seems that the bug community is tuned to the seasonal condition of the host plant rather than the reverse.

Fire is almost as predictable as monsoon rain in the savanna of tropical Australia. Gillon D. (1983) reports that insect abundance in African savanna declines by a factor of three following a fire event and takes 2-3 months to recover. In Australia's tropical eucalypt forest fire initiates a major flush of growth in the ground layer. Other tropical studies have established that fresh leaves are favoured by insects (Reichle *et al.* 1973, Rockwood 1974, Coley 1980, Lowman 1985) and a positive correlation between growth and damage for most species was indicative of this phenomena in this study (Table 6.3). It seems that any negative effects of fire on insect abundance are rapidly compensated by the positive response of insects to fresh foliage. Insect lifecycles may be tuned to the predictable fire period so that they can rapidly recover their numbers. An alternative explanation is that insects move down from the tree canopies to feed on the fresh foliage.

If this migration were occurring, seasonal patterns of the total phytophagous insect community may resemble patterns recorded from elsewhere in the seasonal tropics.

In the African savanna fire not only affects abundance but profoundly influences the composition of the insect community (Gillon D. 1983). The high fire frequency of the tropical eucalypt forest may account for the relatively low numbers of caterpillars and high numbers of mobile insect groups such as the Orthoptera and Hemiptera. Thus, the composition and abundance of the insect community in this environment may be a product of the direct effects of fire and the influence of this force on resource availability and quality. Moisture does not seem to be a severe limitation to plant growth (see Chapters 2 and 3) and the inefficacy of the tropical dry season to depress the insect community in the ground layer of the tropical savanna forest seems to indicate that there is sufficient water in the soil, in plant foliage and in other microsites to satisfy the lifecycle requirements of many insects.

Chilvers and Brittain (1972) and Burdon and Chilvers (1974a) highlight the possibility that parasite preference determines the dominance ratio of *Eucalyptus* subgenera in southeastern Australia. This study provides the opportunity to examine the relevance of insect herbivory to the composition of the tropical forest which are dominated by members of the Australian centred genus *Eucalyptus* despite other tree taxa being widespread and common. The results from this study were somewhat ambiguous in relation to this possibility. The dominant eucalypts in most of the forest across the coastal regions of the Top End are *Eucalyptus miniata* and *Eucalyptus tetrodonta*. These species in the subgenus *Eudesmia* suffer intermediate levels of damage relative to other tree species (Table 6.1) and seem to have relatively low densities of the major insect groups (Fig. 6.3).

While there is no evidence that suppressed growth is a phenotypic response to insect herbivory, the possibility that insect activity has precipitated an evolutionary response cannot be precluded. Insect attack and the prevalence of fire may have been important selective forces promoting a growth limited phenology for woody sprouts in the tropical eucalypt forest. Despite possibilities of evolutionary response

there were no indications from this study that the plant species that presently dominate tropical savanna forest are those that have developed mechanisms to avoid insects. Furthermore, there was no evidence that insects influence growth pattern or vegetation structure. It is more evident that the phytophagous insect community is structured by climatic, fire and plant physiological cycles than spatial or temporal vegetation patterns being controlled by insects.

CHAPTER 7 ECOLOGICAL DETERMINANTS OF SEEDLING SUCCESS IN TROPICAL EUCALYPT FOREST

7.1 Introduction

It is general knowledge that tree germinates are a rare occurrence in the tropical eucalypt forest (Lacey 1974, C. Dunlop, B. Wilson, D. Bowman pers. comm., Fensham pers. observ.). A more prevalent means of regeneration is by vegetative modes such as root suckers and lignotubers (Lacey and Whelan 1976). Dunlop (1988) has suggested that the fire and rainfall climate of the monsoonal tropics disfavours propagation from seed as a regeneration strategy.

Stems that regenerate from underground organs rarely grow continuously and remain as stunted stems in the ground layer (Chapter 3). The previous chapters have focussed on the factors contributing to this dormancy and the consequent low frequencies of saplings in the tropical forest. When the appropriate combination of circumstances prevail, saplings do occasionally leave the ground layer to become overstorey trees. Chapter 5 demonstrated that this sporadic event happens frequently enough to sustain the forest. Regeneration from seed must also occur. Lacey (1974) suggests that a fire free period is necessary for the successful establishment of *Eucalyptus porrecta* seedlings in the eucalypt forest of Melville Island. The factors contributing to the survival of young seedlings and their incorporation into the pool of suppressed woody sprouts in the ground layer are examined in this chapter.

Chapters 3, 4 and 5 provided information on the influence of fire, overstorey competition and micro-habitat conditions on the success of woody sprouts. This chapter examines the influence of these factors on the survival and growth of seedling forest trees. It documents the survivorship of naturally occuring seedlings of *Eucalyptus miniata* and *Eucalyptus tetrodonta* and the response of these seedlings and planted seedlings of a range of open forest species to fire and seasonal stress. The chapter also addresses the hypothese that: a) seedling establishment and growth are influenced by overstorey competition. b) The establishment of seedlings is related to microhabitat conditions.

Chapter 6 suggested that overstorey trees may suppress saplings by allelopathic influences. It has been suggested that foliar insect frass (Silander *et al.* 1983), litter leachates (del Moral and Muller 1970, del Moral et al. 1978) and foliar leachates (del Moral 1969, del Moral *et al.* 1978) from the genus *Eucalyptus* can have allelopathic effects. Part of this chapter explores the allelopathic influence of leaf litter and live leaf leachates from mature trees on seedling growth.

7.2 Methods

7.2.1 Progress of young seedlings

In the early wet season of 1987/88, a sward of *Eucalyptus miniata* and *Eucalyptus tetrodonta* tree seedlings was located. The status of the seedlings could be assured because cotyledonary leaves were evident on most individuals. At this time, a grid comprising 24 2 x 2 m sub-plots was marked within the sward using steel pickets (Fig. 7.1). Over each sub-plot a square frame defining a smaller scale grid comprising 100 20 x 20 cm cells allowed the mapping of each seedling. The position and species of seedlings was noted on the 2/12/87, the 7/3/88, the 5/5/88, the 12/6/88 and the 16/11/88. The dbh, height, crown radii, species and position of all surrounding mature trees was noted. The plot was burnt on the 30/7/88 by a typical dry season fire that incinerated all understorey vegetation but left tree crowns unscorched. A chi-squared test on the proportion of survivors (number of seedlings at the initial assessment divided by the number of seedlings at the final assessment) in each 2 x 2 m cell was performed for each species.

7.2.2 Seedling garden experiment

The open forest species *Terminalia ferdinandiana* (sown 10/87), *Acacia aulacocarpa* (sown 1/87), *Eucalyptus miniata* (sown 9/87) and *Eucalyptus tetrodonta* (sown 7/87) were grown in a Darwin nursery. *Terminalia ferdinandiana* and *Acacia aulacocarpa* were potted in 10 x 10 cm square pots in a potting soil that included 16 g of Osmocote® (N:P:K:S ratio; 18.0:4.8:8.3:3.4), a fertilizer with a longevity of 8-9

months. The other species were grown in tube pots containing 3 g of Osmocote®.

Gardens were established at two nearby sites:

Site 1. Open forest dominated by *Eucalyptus miniata* with occasional *Eucalyptus tetrodonta* and *Eucalyptus nesophila* near Milikapiti.

Site 2. The same forest as Site 1 except the overstorey was killed in advance using the tree poison Tordon® within an area that included a buffer of one crown width around the garden. Eleven *Eucalyptus miniata* trees with a total basal area of 0.28 m^2 were killed.

Each garden was fenced to protect the young plants from ground-dwelling herbivorous mammals. Large woody plants in the ground layer of each garden were removed with a mattock. Wide angle vertical photos were taken from the centre of each garden during the wet season when canopies are most evergreen. Three holes were augered at each site and the soil profiles described. Soil samples were taken from 15 and 45 cm on the 13/6/88 and stored in jars for gravimetric moisture analysis (see Section 2.2.1). To ensure seedling size was evenly distributed between the gardens prior to planting the following technique was employed. The seedlings of each species were ordered from tallest to shortest. One tree from each pair of seedlings along this gradient was allocated to a garden. The seedlings within each pair were rotated on every allocation so that the same garden was not receiving the tallest tree of each pair. Twenty individuals of each species were available for each garden. The fenced boundary of each garden was mapped and a 75 x 50 cm grid established. The plants were randomly allocated to points on the grid and planted between the 23-25/12/87. The trees were measured and their leaves counted on the 4/4/88, the 6/7/88, the 15/11/88 and the 5/12/89. Some grass was removed from around the seedlings in March 1988. The extent of hand weeding mimicked natural gaps in the grass layer. A fire break was burnt around the gardens during the dry season of 1988. This afforded relief from fire until July 1989 when a typical dry season fire incinerated the ground layer vegetation of both gardens.

7.2.3 Association of woody species with vegetation pattern

A 50 x 50 m grid comprising 400 2.5 x 2.5 m cells was established in an area of open forest without obvious edaphic, topographic or floristic variation. In each of the 400 cells the following information was documented:

1) the dbh and species of woody plants taller than 3 m H.
2) The number and species of all trees in the ground layer (<3 m H).
3) The higher plant species rooted in the quadrat and an estimate of their cover on a five point scale (barely present, <5%, 5-10%, 10-50%, >50%).
4) Percentage cover of the surface gravel.

Holes were augered to a depth of 1 m at five points throughout the grid to search for edaphic discontinuities.

The gridcells were classified by the polythetic divisive technique TWINSPAN using quantitative abundance classes (equal weightings) and on the presence-absence of species. The four group level was chosen as a realistic segregation of micro-pattern.

The association of the frequency of eight woody species (*Acacia aulacocarpa, Buchanania obovata, Erythrophleum chlorostachys, Eucalyptus confertiflora, Eucalyptus miniata, Eucalyptus tetrodonta, Planchonia careya, Terminalia ferdinandiana*) with the TWINSPAN groups (using a separate classification that excluded those eight tree species) was tested using the Kruskal-Wallis test. This was performed to test whether the occurence of woody sprouts is associated with micro-environmental cariation as reflected by floristic pattern.

7.2.4 Effects of leaf litter on seedlings

Twenty naturally occurring seedlings of *Eucalyptus miniata* and *Eucalyptus tetrodonta* were mapped adjacent to the seedling plots described in Section 7.2.1. Eucalypt litter was collected in the late dry season (7/3/88) from a fire protected eucalypt forest dominated by *Eucalyptus tetrodonta* and *Eucalyptus miniata*. The forty mapped seedlings were mulched with this litter to a depth of 5 cm and radius of

about 25 cm. Care was taken to ensure seedlings were not smothered by leaf litter. A further 20 individuals of each species were left unmulched to serve as a control and the height and number of leaves of all plants in the experiment were measured. The seedlings were remeasured after two months and their mortalities, heights and number of leaves compared between mulched and control treatments using the chi-squared and Mann-Whitney U-tests respectively.

7.2.5 Allelopathic effects of *Eucalyptus tetrodonta* leaves on tree seedlings

Plants of the open forest tree species *Acacia aulacocarpa* (sown 1/87), *Terminalia ferdinandiana* (sown 10/87), *Eucalyptus miniata* (sown 9/87), *Eucalyptus tetrodonta* (sown 7/87) and the grass *Sorghum plumosum* (sown 12/87) were germinated in seed trays. They were potted into small tubes and subsequently into 150 cm diameter pots where they were allowed to establish for at least 30 days. Stem length and number of leaves of all plants (only the latter measure for *Sorghum plumosum*) was assessed and the plants were ordered and separated into two treatments using the method described in Section 7.2.2 that aims for an even size distribution between treatments. With the exception of *Acacia aulacocarpa* and *Eucalyptus miniata* the experiment commenced for all species on the 11/1/88. Treatment for the former species was started on 2/4/88. Twenty individuals of each species were subjected to the following treatments:

Leaf treatment Leaves from a freshly fallen *Eucalyptus tetrodonta* were collected and shredded to the consistency of tea leaves. This mulch was placed around the young plants to a depth of 1 cm.

Control treatment The leaf treatment was mimicked using an inert potting substance known as Vermiculite®.

The pots were placed in the full sun and surrounded by a buffer of soil filled pots. The experiment was saturated by water sprinklers in the morning and afternoon of every day. Final measurements of *Eucalyptus tetrodonta* and *Terminalia ferdinandiana* were made on the 1/4/88. *Acacia aulacocarpa* and *Eucalyptus miniata* were measured on the 2/6/88. These measurements determined the stem length and number of leaves for all tree species. The above-ground biomass of

Sorghum plumosum was oven dried at 100° C for 48 hours and weighed. Differences between treatments for the initial and final biomass assessments were determined using the Mann-Whitney U-test. Mortality differences between treatments were compared using the chi-squared test.

7.3 Results

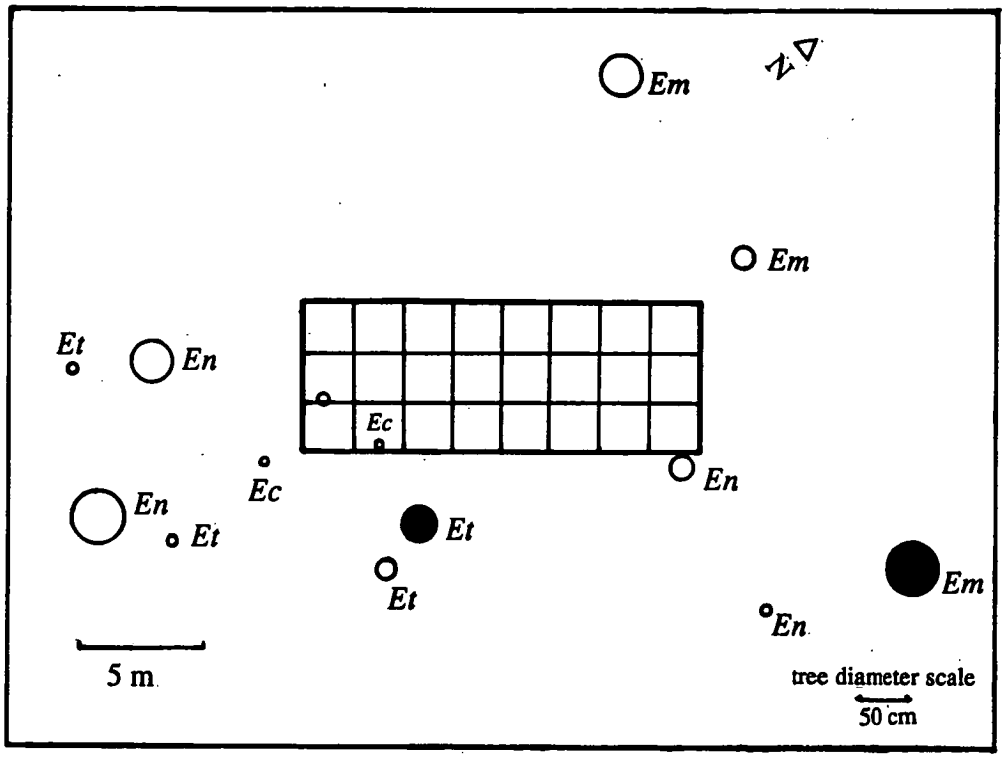
7.3.1 Progress of young seedlings

The *Eucalyptus miniata* and *Eucalyptus tetrodonta* parent trees of the germinating seedlings are marked on Fig. 7.1. These trees were obvious because of the abundance of mature fruits under their canopies and the absence of fertile material on other trees in the vicinity. The crown radii of the *Eucalyptus miniata* and *Eucalyptus tetrodonta* mother trees were approximately 6 and 4 m and their heights 15 and 12 m respectively. It is evident from Fig. 7.1 that seed can disperse at least three crown widths and 1.5 times the height of the parent tree.

New seedlings appeared during the course of this study although the mapping procedure did not allow this recruitment to be quantified. Recruitment of new individuals accounts for the increased numbers of *Eucalyptus tetrodonta* seedlings in the interval between the third and fourth samples (Fig. 7.2).

Attrition of seedling numbers seems to occur at a constant rate despite the influence of the dry season and a fire (Fig. 7.2). Furthermore, there is no apparent preferential survival of seedlings in areas of lower competitive influence from overstorey trees. This is suggested by a non-significant chi-squared result for the association of survivorship in the cells of the macro-grid ($P>0.05$).

Seedlings excavated in April 1988 had developed a rudimentary lignotuber during the six months following germination (Plate 7.1).



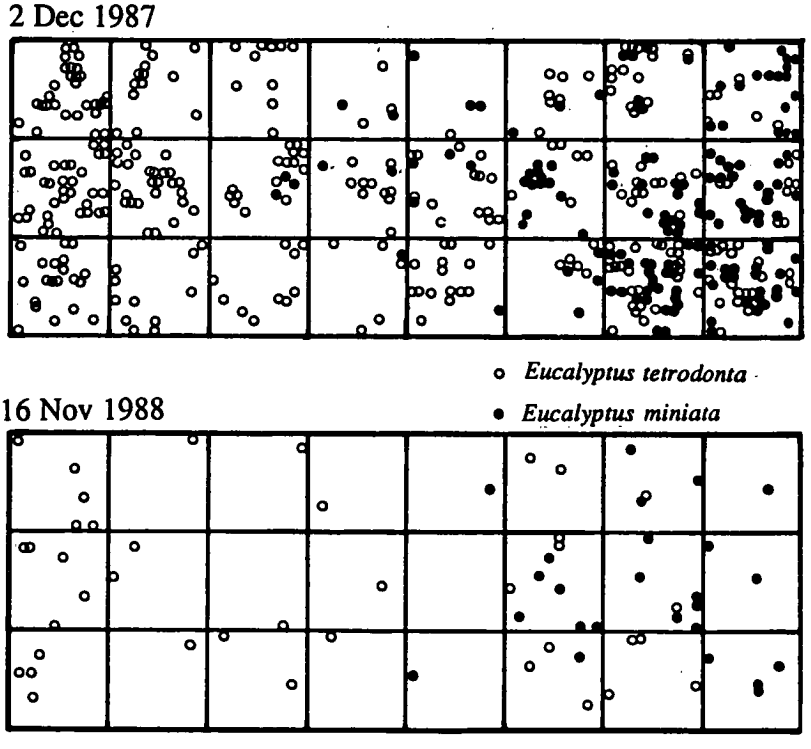


Figure 7.1 Plan of surrounding trees (*Ec Eucalyptus confertiflora, Em Eucalyptus miniata, En Eucalyptus nesophila, Et Eucalyptus tetrodonta*) and germinates across the study plot at the initial and final sampling time. The mother trees of the seedlings are blacked out.

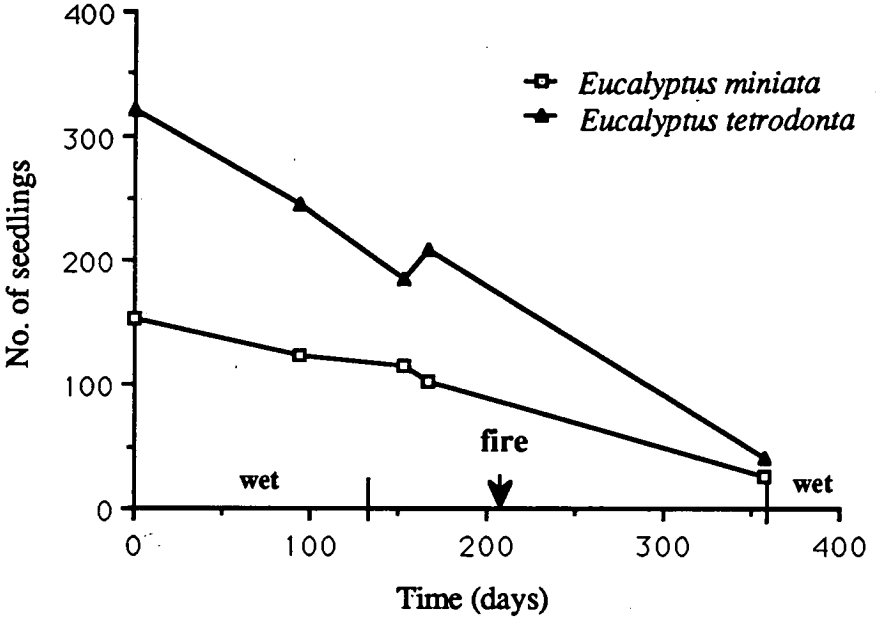


Figure 7.2 Mortality of tree seedlings within the study grid (96 m^2).

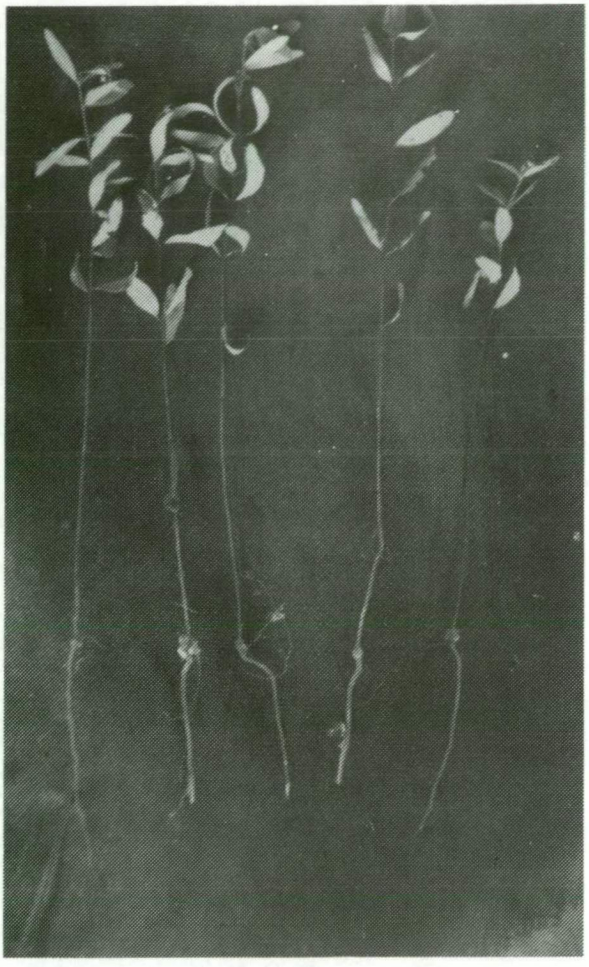


Plate 7.1 Young *Eucalyptus miniata* seedlings. Note the lignotuberous swellings and deep tap root.

7.3.2 Seedling garden experiment

Shade levels were 40% over the live eucalypt forest garden and 30% over the dead eucalypt forest garden as estimated by comparison with the crown figures provided in McDonald *et al.* (1984).

Both gardens occur on a grey, yellow, brown loamy sand. Nine percent gravel in the surface layer increases to about 15% at 45 cm and a very dense gravel bed occurs at 70 cm. Soil texture was constant to this depth. The mean gravimetric soil moisture content for the gravel free portion of the surface soil at each site is presented in Table 7.1 and there appears to be little difference between sites. Evidence from the tree killed plots in the competition experiment showed that significant increase in soil moisture after tree killing only occurred at depths greater than 90 cm (Section 5.3.3).

Table 7.1 Gravimetric moisture content of the gravel free soil portion in the eucalypt forest and tree killed gardens.

	mean	s.e.m.	n
Site 1 Eucalypt forest			
15 cm	4.17	0.19	3
45 cm	6.04	0.16	3
Site 2 Tree killed eucalypt forest			
15 cm	4.61	0.28	3
45 cm	6.08	0.19	3

There was no statistically significant difference in the starting heights or number of leaves of seedlings for any species between gardens. For the final analysis the number of leaves reflects the height of the young trees and only the latter results are presented. All four open forest tree species are taller under dead trees than live overstoreys and this result is statistically significant at the final measurement for *Terminalia ferdinandiana* ($P<0.01$), *Eucalyptus tetrodonta* ($P<0.02$), *Eucalyptus miniata* ($P<0.001$)(Fig. 7.3). These results are essentially mirrored by

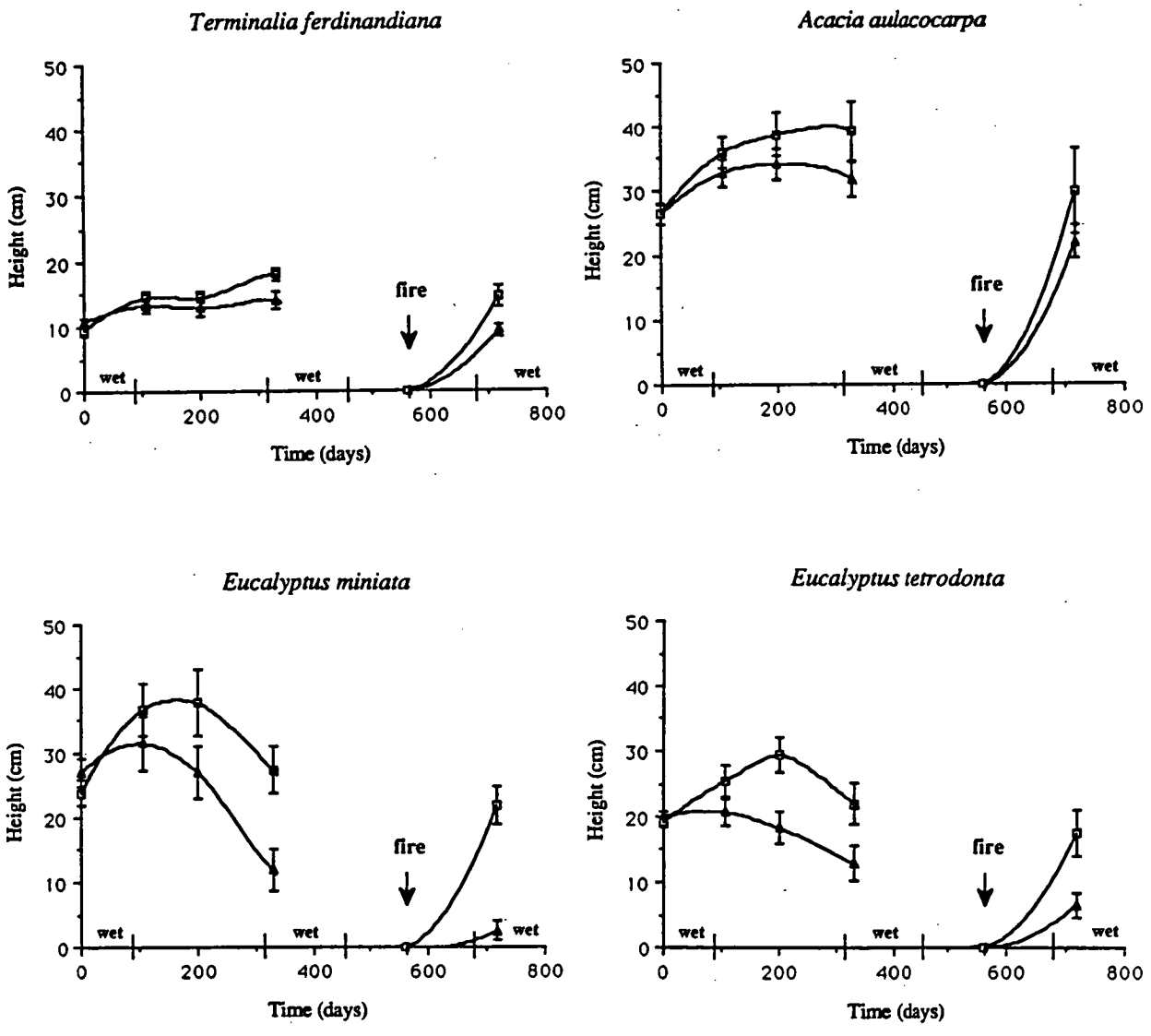


Figure 7.3 Mean height (and s.e.m.) of tree seedlings in the eucalypt forest garden (♦) and the tree killed garden (□).

the survivorship of seedlings at each site with the exception of *Terminalia ferdinandiana* which suffered equal mortailty in both treatments (Fig. 7.4). All species were able to survive fire although *Eucalyptus miniata* suffered considerable and steady mortalities under the live canopy. The mortality of this species was greatest during the late dry season-early wet season period one year after planting and declined in the second dry season during which period the gardens were burnt (Fig. 7.4).

7.3.3 Association of woody species with vegetation pattern

The microscale vegetation patterns revealed by classification of presence-absence and abundance floristic data were very similar. This was also the case with the results of statistical tests that used the groups from both schemes as samples. A presence-absence scheme, including all higher plant species is chosen for presentation (Fig. 7.5, Table 7.2).

The percentage frequency of the species by classificatory group is presented in Table 7.2. The four classificatory groups form distinct patches on the grid (Fig. 7.5) suggesting they are associations with ecological reality. The soils were uniform across the grid at the resolution of field assessment (McDonald *et al.* 1984). They consisted of brown loam in the surface horizon that graded to red loam between 5 and 15 cm. Soil texture was constant to 50 cm where the soils became gradually more clayey with depth. Surface gravel was mostly less than 5% and always less than 10% cover. Gravel content through the profile was low. The mean frequency of woody sprouts of the eight tested tree species by classificatory groups (derived independently of the distribution of these tree species) is presented in Table 7.3. It is evident that the distributions of *Acacia aulacocarpa, Buchanania obovata, Erythrophleum chlorostachys, Eucalyptus miniata* and *Eucalyptus tetrodonta* are related to the overall floristic pattern.

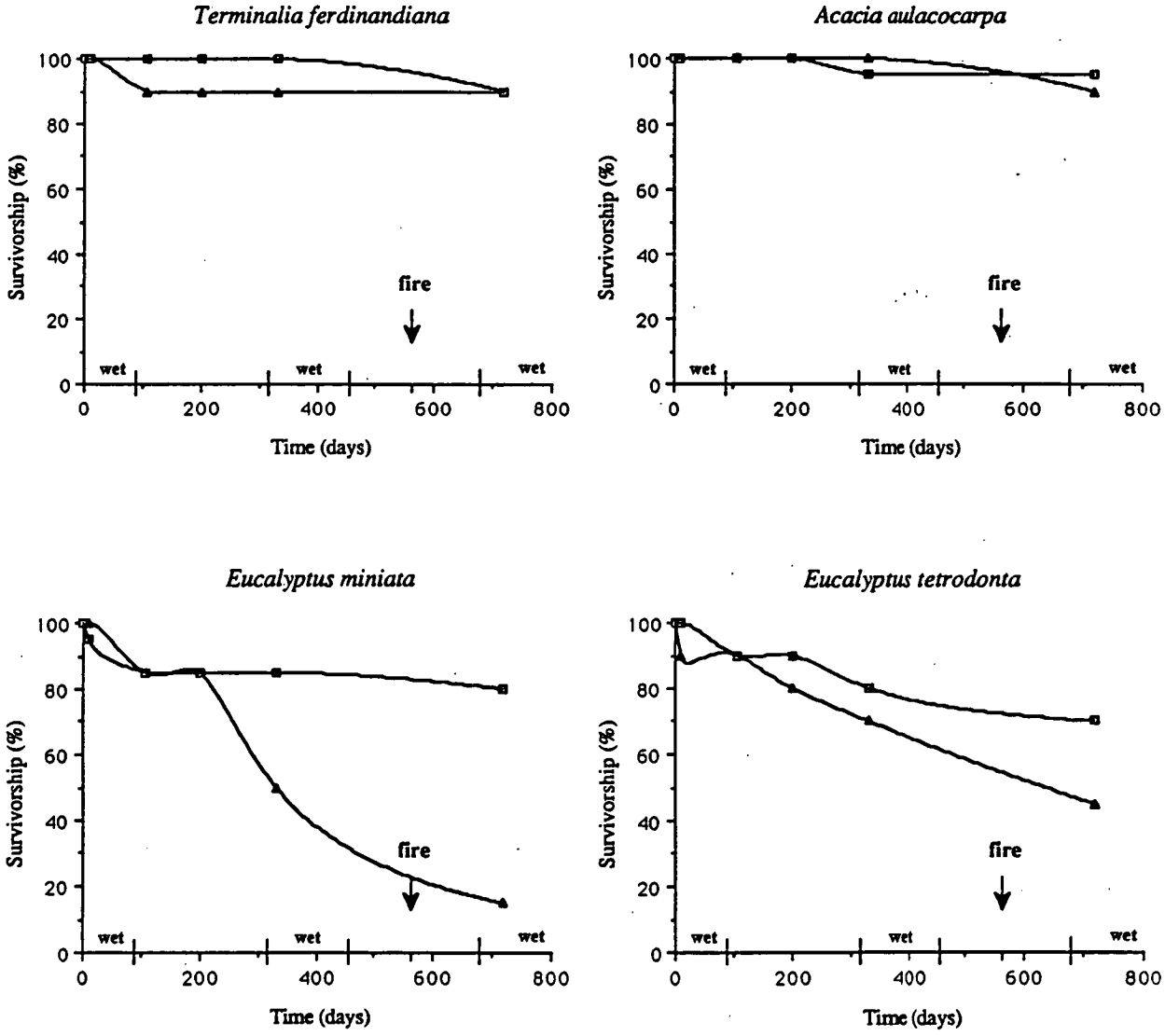


Figure 7.4 Mortality of tree seedlings in the eucalypt forest garden (♦) and the tree killed garden (□).

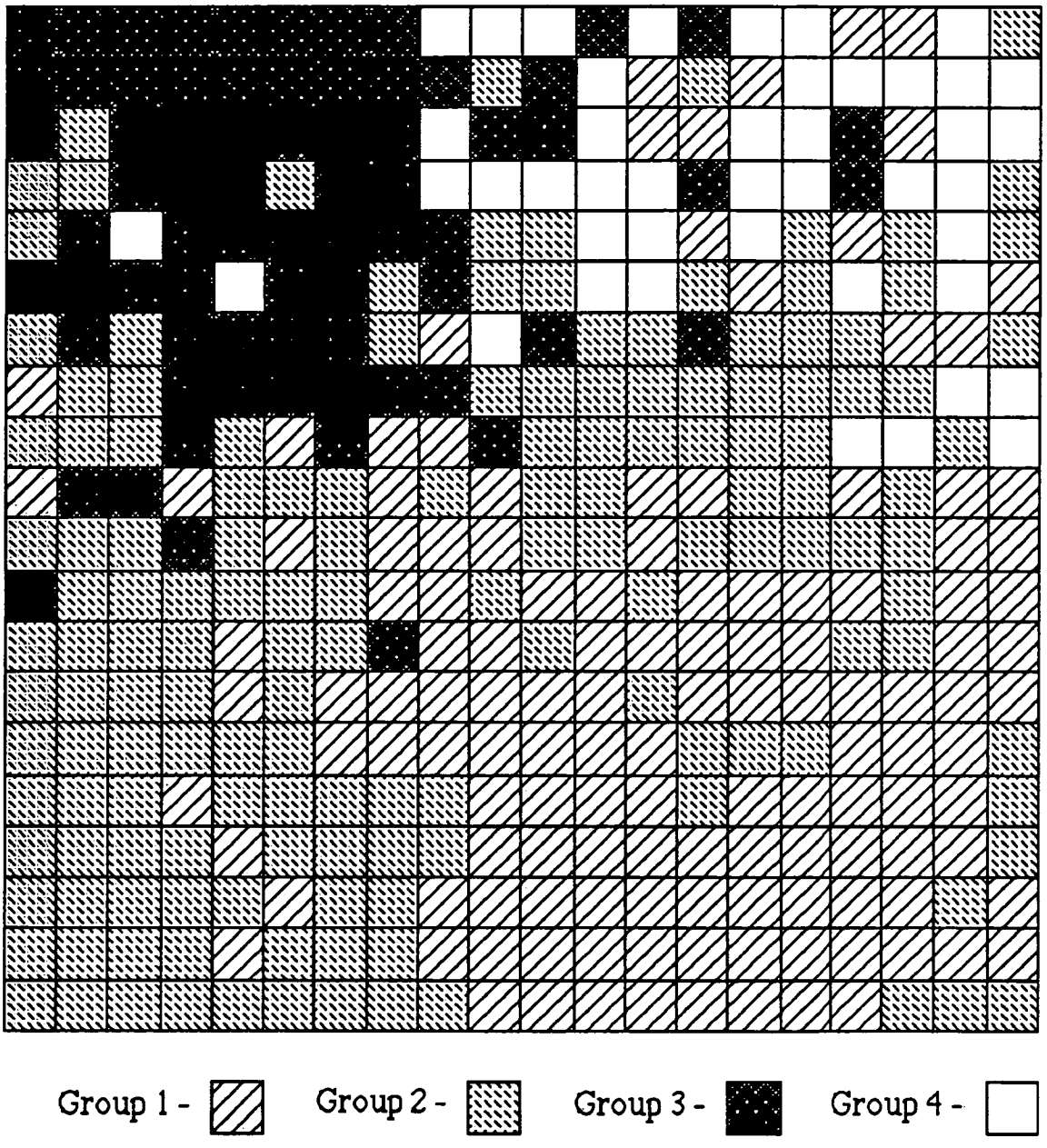


Figure 7.5 Distribution of TWINSPAN classificatory groups in 0.25 ha of open eucalypt forest on Melville Island.

Table 7.2 Percentage frequency of higher plant species in the TWINSPAN classificatory groups of 400 contiguous quadrats in 0.25 hectares of open eucalypt forest on Melville Island. Only species with greater than 20% frequency in any one group are included.

	TWINSPAN GROUP			
Species	1	2	3	4
Uraria lagopodioides	40.2	7.3	6.9	6.8
Goodenia leiosperma	59.1	21.9	4.1	0.0
Mitrasacme sp.	50.0	10.6	24.7	13.6
Polygala eriocephala	31.1	14.6	12.3	9.1
Eucalyptus tetrodonta	63.6	66.9	9.6	2.3
Rostellularia pogonathera	42.4	28.5	28.8	27.3
Spermacoce sp.	81.8	67.6	46.6	52.3
Thaumastochloa major	62.9	56.3	38.4	43.2
Grevillea decurrens	34.1	22.5	16.4	0.0
Planchonia careya	52.3	50.3	43.8	29.6
Eriosema chinensis	12.8	11.9	4.1	2.3
Eucalyptus porrecta	15.2	13.9	9.6	2.3
Polygala orbicularis	37.1	44.4	26.0	11.4
Galactia tenuiflora	3.0	31.1	2.7	0.0
Murdannia gigantea	21.2	38.4	23.3	15.9
Acacia leptocarpa	23.5	37.1	28.8	15.9
Pachynema complanatus	68.9	70.8	67.1	61.4
Eulalia mackinlayi	91.7	92.1	95.9	81.8
Flemingia parviflora	47.7	50.3	52.1	59.1
Alloteropisis semialata	99.2	100.0	100.0	100.0
Chrysopogon fallax	98.5	99.3	100.0	100.0
Eucalyptus miniata	53.8	52.3	46.6	52.3
Pseudopogonatherum contortum	46.2	9.9	6.9	54.6
Acacia aulacocarpa	40.9	58.3	61.6	52.3
Livistona humilis	31.8	41.1	46.6	50.0
Hibbertia cistifolia	60.6	55.6	76.7	79.6
Buchanania obovata	56.1	65.6	78.1	75.0
Eucalyptus nesophila	56.8	56.3	69.9	61.4
Eriachne avenacea	11.4	29.1	95.9	63.6
Sauropus glaucus	10.6	8.6	35.6	18.2
Desmodium sp. 'clavitricha'	47.0	64.2	78.1	20.5
Cycas armstrongii	14.4	17.2	45.2	20.5
Sorghum plumosum	43.2	43.1	78.1	25.0
Helicteres sp.	0.0	6.6	26.0	0.0
Erythrophleum chlorostachys	77.3	59.6	38.4	93.2
Persoonia falcata	18.9	9.3	8.2	25.0
Eucalyptus confertiflora	8.3	26.5	28.8	45.4
Gardenia suffruticosa	9.1	39.1	11.0	56.8
Alphitonia excelsa	9.1	13.3	5.5	22.7
Cheilanthes sp.	11.4	6.0	48.0	56.8
Indigofera saxitilis	16.7	4.6	20.6	45.5
Phyllanthus sp.	15.9	11.9	0.0	20.5
Crotolaria montana	3.0	8.6	4.1	31.8
Number of Quadrats	132	152	72	44

Table 7.3 Frequency of ground layer woody sprouts of eight common tree species according to a TWINSPAN classification that did not include those eight species. Significant differences according to the Kruskal-Wallis test are indicated.

	TWINSPAN GROUP				
Species	1	2	3	4	Significance
Buchanania obovata	0.79	0.94	1.15	1.41	P<0.05
Planchonia careya	0.91	0.79	0.60	0.56	NS
Terminalia ferdiandiana	0.12	0.19	0.19	0.10	NS
Erythrophleum chlorostachys	1.72	2.47	1.27	4.31	P<0.001
Eucalyptus tetrodonta	1.84	1.84	0.49	1.08	P<0.001
Eucalyptus miniata	0.47	0.79	0.55	0.73	P<0.05
Eucalyptus confertiflora	0.28	0.20	0.36	0.41	NS
Acacia aulacoacarpa	1.21	1.31	2.23	1.59	P<0.01

7.3.4 Effects of leaf litter on seedlings

Two-hundred and thirteen mm of rain fell at Nguiu (10 km distant) during the 2 months between the initial and final seedling measurements. This rainfall should have ensured that litter leachates were well washed through the seedling root zone.

There was no significant difference in the initial and final heights or number of leaves between treatments for *Eucalyptus miniata* and *Eucalyptus tetrodonta* seedlings (P>0.05 in all cases). There was also no significant difference in mortality for *Eucalyptus tetrodonta* (control- 15%; litter- 10%) or *Eucalyptus miniata* (control- 20%; litter- 25%)(P>0.05).

7.3.5 Allelopathic effects of *Eucalyptus tetrodonta* leaves on tree seedlings

There was no significant difference in initial height or numbers of leaves for any species between treatments (P>0.05). Mean heights and numbers of leaves at the final measurement and the significance of differences between treatments is presented in Table 7.4. Mulch from leaves of mature *Eucalyptus tetrodonta* significantly inhibits seedlings of the same species (P<0.01). The Mann-Whitney U-test comparing height of *Eucalyptus tetrodonta* seedlings between treatments does not

Table 7.4 Mortality, mean height and numbers of leaves of four open forest tree species and the mortality and biomass of *Sorghum plumosum*, according to treatment. Probabilities for differences between treatments for mortality are from the chi-squared test and from ANOVA for height and number of leaves.

	Mulch treatment		
	Vermiculite control	*Eucalyptus tetrodonta* leaves	Significance
Terminalia ferdinandiana			
Mortality (%)	0	5	NS
Height (cm)	14.9	17.7	P<0.05
Number of leaves	14.4	14.4	NS
Acacia aulacocarpa			
Mortality (%)	5	5	NS
Height (cm)	10.4	10.3	NS
Number of leaves	9.5	9.1	NS
Eucalyptus tetrodonta			
Mortality (%)	20	75	P<0.02
Height (cm)	14.1	6.9	P<0.01
Number of leaves	18.1	3.6	P<0.001
Eucalyptus miniata			
Mortality (%)	5	5	NS
Height (cm)	37.9	43.8	NS
Number of leaves	15.9	16.1	NS
Sorghum plumosum			
Mortality (%)	0	5	NS
biomass (g)	20.0	15.4	P<0.05

reflect the mortality of this species because the heights of the survivors (mean=27.6 cm) tended to be greater than the survivors in the control treatment (mean=17.6 cm). Fifteen individuals were killed within 6 weeks compared to four deaths in the control (P<0.02). Other open forest tree species were not inhibited by *Eucalyptus tetrodonta* leaves (Table 7.4). In fact *Terminalia ferdinandiana* showed a slight increase in height (P<0.05) under the mulch which may be a consequence of nutrient enhancement. The biomass of *Sorghum plumosum* declined significantly with the addition of live *Eucalyptus tetrodonta* leaf mulch (P<0.05).

7.4 Discussion

The survivorship of young seedlings is difficult to determine in this study because of some seedling recruitment after the initial germination event. However the maximum survivorship can be calculated and was 83.8 % for *Eucalyptus miniata* and 87.2 % for *Eucalyptus tetrodonta* after 12 months. Survivorship of young seedlings did not seem to be favoured on ground where competition from the overstorey is likely to be less intense.

The establishment of tree seedlings may also be affected by microscale environmental variation. The occurrence of some tree species in the ground layer of the tropical forest was associated with overall floristic pattern. There were no obvious disjunctions in edaphic conditions. However, the cause of these small-scale patterns may be subtle variations in the soil environment. *Sorghum intrans* forms distinct patches in the open forests of the Top End. Andrew (1986) concluded that these patches are a result of small-scale variation in edaphic conditions. He reports slight but significant variations in soil moisture content and nutrient status that were not evident from cursory investigation of soil physical characteristics.

Young germinates of *Eucalyptus miniata* and *Eucalyptus tetrodonta* rapidly develop a lignotuber and a deep root system (Plate 7.1). These adaptations allow survival through the inevitable fire and drought of the oncoming dry season. The underground parts of nine month old tree seedlings endured the heat of a dry season fire and regenerated new stems. These stems grew rapidly. Seedlings planted in the gardens grew more rapidly during the late dry season, after fire had removed the above-ground biomass, than during previous times (Fig. 7.3). This growth pattern is similar to that exhibited by naturally occurring, well established woody sprouts in the tropical eucalypt forest (Chapter 3). The perreneating organs and deep root systems allows for the rapid replacement of above-ground biomass. The young tap root attains sufficient depth to access regions of the soil profile where moisture is available through the dry season in this forest type (see data on moisture availability in section 2.3.3). The fact that the rate of mortality through the dry season is no greater than for other periods

without fire and with more favourable moisture conditions exemplifies the success of these adaptations. The ability of open forest seedlings to cope with fire is verified by the survival of 2 year old trees in the eucalypt forest garden following a dry season fire. *Acacia aulacocarpa* and *Terminalia ferdinandiana* were especially resilient to fire and the *Eucalyptus* species suffered lower mortalities over the fire period than during other times (Fig. 7.4).

Allelopathic mechanisms may be important in the tropical eucalypt forest. If these mechanisms are occurring they do not seem to be the result of litter leachates as mortality was not significantly effected by mulching with leaf litter. However, the nursery experiment showed that leachates from living plant material can cause mortality. This was evident from the death of *Eucalyptus tetrodonta* seedlings under the mulch of fresh leaves of the same species.

It is necessary to be extremely cautious inferring ecological reality on this experimental result. Leaf leachates washed from canopies by rain would be considerably more dilute and of a different composition than the leachates of chopped leaves used in this experiment (May and Ash 1990). However, the field gardens verified the indication of intraspecific suppression from the nursery experiment. Young plants of *Eucalyptus miniata* suffered severe mortality in a forest dominated by the same species but had survival rates comparable to other open forest species where the canopy had been killed. The competitive influence of *Eucalyptus miniata* canopy trees did inhibit other open forest species as indicated by the significantly slower growth rate of all seedlings (Fig. 7.3) and the higher mortality of *Eucalyptus tetrodonta* under the live *Eucalyptus miniata* canopy compared to the tree killed plot (Fig. 7.4). However, inhibitory effects were most dramatic for *Eucalyptus miniata* seedlings under the canopy of the same species.

Intraspecific allelopathy has been demonstrated for *Pinus radiata* (Lill and Waid 1975, Chu-Chou 1978) and *Grevillea robusta* (Webb *et al.* 1967). Bevege (1968) suggests that the autotoxicity of *Araucaria cunninghamii* may contribute to the suppression of regeneration in forests dominated by this species. Florence and Croker (1962) have demonstrated that microbes in the soil of blackbutt (*Eucalyptus*

pilularis) forest inhibit the growth of blackbutt seedlings. Evans *et al.* (1967) isolated a mechanism for this allelopathic interaction by demonstrating that phytotoxins produced by a fungal inhabitant of blackbutt root surfaces inhibit seedlings of that species.

The data presented here does indicate that antagonistic chemicals are produced by at least one *Eucalyptus* species of the tropical forest. It is difficult to implicate allelopathy as the agent of competitive suppression in the garden experiment. However, both the field and garden experiment indicate that competitive interaction in these forests is particularly potent between members of the same species. The specificity of this competitive relationship is more easily attributed to an allelopathic mechanism involving chemical substances with a specific action than to competition for edaphic resources. Chapter 6 argued that the invocation of allelopathy as an agent for the suppression of sapling regrowth by overstorey trees is consistent with the available evidence. This study has provided some positive evidence of this mechanism from a controlled experiment.

Codominance of *Eucalyptus* species without obvious environmental separation is a notable feature of tropical open forest (Chapter 2). If intraspecific allelopathy does control regeneration in the savanna forest it may provide a balancing mechanism between coexisting dominant tree species. Intraspecific allelopathy would contribute to the maintenance of codominance because establishment and regeneration of a dominant species would be inhibited and the regeneration of sub-dominant species favoured. If this mechanism occurs it is predicted that the relative dominance of tree species may be cyclic. This mechanism could explain the stand structure of the forest described in Chapter 5. In that instance *Eucalyptus tetrodonta* seems better placed to increase its abundance than *Eucalyptus miniata* in a forest dominated by the latter species.

CHAPTER 8 GENERAL DISCUSSION

8.1 Summary of findings and conclusion

Previous studies in monsoonal Australia have sought to understand vegetation-environment relations using multivariate analyses of floristic data and correlative techniques. Individual plant communities have been recognised by their distinctive flora and overstorey dominants. At the scale of community separation, the underlying environmental determinants have been successfully recognised (eg. Bowman and Minchin 1987, Kirkpatrick *et al.* 1987). However, there is considerable variation within plant communities. This is particularly true for the eucalypt formations that dominate the vast majority of northern Australia. Within this vegetation there is a complex of intergrading combinations of structural variants, understorey types and overstorey dominants. With the exception of Bowman *et al.'s* (1990) study of micro-pattern within a eucalypt woodland near Katherine, no previous studies have attempted to understand the environmental determinants of vegetation pattern at the sub-community scale.

Chapter 2 sought to distinguish between open vegetation patterns that could be explained in terms of edaphic or climatic influence and those patterns that were unrelated to these controls. The introduction to this chapter suggested that correlative studies using simple environmental measures over small scale vegetation pattern would fail. It was suggested that structural changes may be determined by edaphic conditions at soil depths that are inconsequential to general floristic pattern. Furthermore, some patterns may result from seasonal cycles of moisture availability that cannot be assessed by temporally constrained studies. It was further suggested that physical environmental features may have interactive effects on moisture conditions that directly influence plant growth. Determination of soil matric potential in a range of open vegetation communities was attempted in order to get a unified measure of these interactive effects.

The precise soil moisture conditions that separate individual plant communities can be identified. *Eucalyptus bleeseri* woodland occurs on sites that have little available moisture during the dry season and *Melaleuca viridiflora* woodland occurs on sites almost as dry as the *Eucalyptus bleeseri* woodland in the dry season but with shallow watertables in the wet season. The widespread evergreen forest formation is dominated on Melville Island by admixtures of *Eucalyptus miniata, Eucalyptus nesophila* and *Eucalyptus tetrodonta* and occurs on sites without extreme moisture regimes.

While soil moisture conditions can be successfully quantified, the assumption that tree roots have equal access to this environment across the range of structural soil types is invalid. In some situations favourable moisture conditions cannot be accessed. Moisture is constantly available throughout the soil profile under semi-deciduous low forest. However, this vegetation type can be separated from the evergreen forest because it occurs on heavy soils that impede root growth.

It is difficult to determine the environmental reasons for variation within the evergreen forest. Some phytosociological gradients occur in association with soil catenas. It is probable that edaphic determinants contribute to these vegetation patterns. However, some changes in vegetation structure and overstorey composition within the evergreen forest cannot be correlated with soil changes. This verifies Bowman *et al.'s* (1990) conclusion that historical coincidence of fluctuating exogenous and endogenous controls precipitate certain patterns. It is suggested that important exogenous controls include edaphic conditions, fire and cyclones. The endogenous factors that potentially interact with these factors include population structure, phenology and competitive interactions.

A preliminary investigation of these interactions involved examination of growth rates across a gradient from evergreen forest to semi-deciduous low forest (Chapter 3). This study reinforced some of the indications provided by the gradient study. It established that moisture availability during the dry season is probably not an important cause of woody vegetation pattern within the eucalypt

forest. The importance of the dry season had been suggested by previous authors (Specht *et al.* 1977, Bowman 1986, 1988, Dunlop 1988). However, it is clear that growth of woody sprouts in the ground layer of the tropical savanna forest does not occur in concert with available soil moisture. Woody sprouts are burnt back to ground level by regular dry season fires. They emerge soon after and grow rapidly during the driest part of the year. By the onset of the wet season growth has virtually ceased and most stems remain dormant until the following dry season. If stems are not razed by fires during this time they either remain dormant or die back to ground level. This growth pattern is essentially uniform for the eight measured tree species across a gradient from evergreen forest to semi-deciduous low forest. However, growth was generally more limited in the low forest than the forest. This verifies that the relatively heavy soils of the low forest are less suitable for growth than the well drained soils of the forest. However, the slow growth of some tree species in the low forest is difficult to equate with their occupation of the canopy in this vegetation type and their relatively rapid growth in the forest, where they are confined to the ground layer. The species in this category, along the gradient studied here, were the deciduous species *Terminalia ferdinandiana* and the semi-deciduous species *Erythrophleum chlorostachys* and *Eucalyptus confertiflora*. The evergreen growth form of the tall eucalypts that dominate the forests cannot be supported without deep root development (Section 2.3.4). This is not possible on the clay soils that support the semi-deciduous low forest. The exclusion of the evergreen species may be the factor that allows the development of tree species in the low forest that are confined to the ground layer in the forest. Further evidence for this mechanism will be discussed in a later part of this discussion.

Sarmiento *et al.* (1985) discuss growth dormancy of woody savanna plants during the wet season. They suggest that the avoidance of insect herbivory is a possible explanation of this strategy. This hypothesis was tested in Chapter 6 and it is suggested that above-ground herbivory cannot adequately account for a growth limited phenology. Neither insect abundance (Section 6.3.3) or herbivory levels (Section 6.3.1) were particularly intense during seasons when stems were dormant. Despite this pattern, it is recognised that insect herbivory may have

been a selective force in the past that has favoured the evolution of limited growth.

Occasionally stems grow continuously and saplings develop. However, the occurrence of these breakaway stems is intermittent even with protection from fire or release from competition. In a fire protected forest at Munmalary, there was no significant sapling development of the overstorey eucalypts and most other tree species (Bowman *et al.* 1988a). Chapter 4 examined the effect of fire protection at another site and demonstrated that saplings will develop in some fire protected situations. The contrasting effect of fire protection at these two sites was attributed to different edaphic conditions. Chapter 4 verified the importance of interactions between site factors and fire history for determining structural patterns at the meso-scale in north Australian savanna.

Evidence regarding the importance of overstorey competition is somewhat ambiguous. There is no doubt the overwood does have an inhibitory effect. Regenerating trees of some species have a propensity to occur in natural gaps within the forest and saplings have developed on some old clearfelled blocks on Melville Island (Section 5.3.4). However, the response of woody sprouts to canopy release is not spontaneous and new saplings were only barely evident on 3 year old experimental sites designed to examine the influence of overstorey trees, acacias and ground layer herbage on regeneration (Section 5.3.3). Furthermore, saplings of some tree species such as the rhizomatous tree *Eucalyptus tetrodonta* showed no association with natural canopy gaps. It seems that overwood suppression is a reality in tropical eucalypt forest but that only a small proportion of stems are capable of responding to competition release. The multi-aged appearance of the regenerating stems on the old clearfelled sites confirms that sapling response has been intermittent (Section 5.3.4).

There are threads of evidence throughout this thesis that contribute to an understanding of the suppressive mechanisms. Sub-surface moisture regimes in the relatively light soils under the evergreen forest are not usually drier than wilting point at the driest time of the year (Section 2.3.3). The fact that extension growth occurs during this

time suggests that soil droughtiness is not limiting growth in these soils (Section 3.3.1). Furthermore, woody sprouts showed little response to increases in soil moisture after overwood removal (Section 5.3.3). These facts indicate that competition for soil water cannot adequately explain regrowth suppression.

Above-ground herbivory is an unlikely explanation for the absence of saplings in the open forest. The reasons for this assertion are firstly that stems protected by insecticide showed no growth response (Section 6.3.2). Secondly, there was no apparent relationship between sapling success and low levels of herbivory (Section 6.3.1). Finally, levels of herbivory are average compared to other Australian forest (Section 6.4.1). Thus the pronounced lack of midstorey in the tropical eucalypt forest does not correspond with relatively high levels of herbivory.

Several treatments were imposed on woody sprouts in attempts to precipitate a growth response. There was virtually no response within 3 years to fire protection (Section 3.3.1), fertilization (Section 3.3.5), relief from competition (Section 5.3.3) and protection from insect grazing (Section 6.3.2). These plants replace their stems when they have senesced or are incinerated by fire. Following limited regeneration, stems remain dormant regardless of fluctuations in the external environment. For the vast majority of woody sprouts it seems that growth mat be limited by the phsiology of the underground organs.

The occasional plants that do exploit a regeneration opportunity may be the only individuals that are physiologically suitable. Examination of the lignotubers of the suppressed ground layer stems suggested that lignotuber size and root system development are critical determinants of regeneration potential (Section 5.3.5). It seemed that plants of middle age with well developed root systems represent the stock of potential trees. Because regeneration from seed only occurs sporadically, there are not surplus stems of all ages. Root system development may be inhibited by herbivory and excavations of these plants revealed substantial damage by subterranean insects (Section 5.3.5). It is suggested that a principal determinant of resource

limitation is the extent of the root system rather than the intrinsic poverty of the soil.

If the repair and maintenance of underground parts is an important priority for woody plants it may provide a partial explanation for the dormancy of foliar meristems during periods that are apparently favourable for growth. The most efficient use of photosynthates during dormant phases may be for the repair and maintenance of the root system. Extension growth that cannot be sustained by an adequate root system is futile. This is particularly true in an environment that is ravaged by annual fires. Seasonal patterns of insect abundance suggest that sap is actively flowing during a period of extension growth dormancy. Previous studies have correlated the abundance of sucking insects with periods of sap flow (ie. Wolda 1978, 1989). In this study, Hemiptera were most abundant during the two dry season sampling periods. While the later part of this season coincides with a period of extension growth the early dry season is a period of stem dormancy. The reliance of sucking insects on flowing sap and their relative abundance during the early dry season is indicative of sap movement despite stem dormancy. Thus, the seasonal pattern of these insects supports the suggestion that photosynthates are being directed to underground organs during the early part of the dry season.

It was suggested earlier that species that rarely realise their potential as trees but are particularly abundant in the ground layer of tropical eucalypt forest may be suppressed through the competitive influence of the evergreen canopy dominants. All four savanna tree species grown in experimental gardens attained less height under a live eucalypt canopy than in a situation where overwood competition was relieved (Section 7.3.2). However, the abundance and diversity of tree species in the ground layer of the evergreen eucalypt forest suggests that interspecific competition is not severely limiting the establishment of these tree species. If dominant evergreen eucalypts suppress the development of other tree species as canopy members it must occur at the sapling stage. For *Erythrophleum chlorostachys* there was evidence of sapling suppression by the dominants of the eucalypt forest. Saplings of this species were clearly associated with canopy gaps in an area of forest on Melville Island (Section 5.3.2).

In the experimental garden the suppressive influence of the eucalypt canopy was most evident for seedlings of the dominant tree species. The canopy species in the garden with live overstorey was *Eucalyptus miniata* and the seedlings of this species suffered severe mortality in this plot (Section 7.3.2). The potency of an intraspecific effect was evident in a pot experiment where leachates from fresh *Eucalyptus tetrodonta* leaves caused significant seedling mortality of this species while other savanna trees seemed unaffected (Section 7.3.5).

If intraspecific allelopathy inhibits sapling regeneration in the eucalypt forest it would explain some features of vegetation pattern. Saplings of the dominant canopy species would be suppressed and the development of other tree species favoured. This mechanism suggests temporal shifts in the dominance ratios of the tree species constituting the forest canopy. There is some evidence for this process provided by the stand structure of a typical eucalypt forest near Paru on Melville Island (Section 5.3.1). Saplings of the main canopy dominant *Eucalyptus miniata* were sparse and the demography of this species suggested that its current dominance would not be maintained. The relative abundance of pole sized *Eucalyptus tetrodonta* suggests that this species is poised to become more dominant as the forest develops.

This thesis argues that overwood competition for nutrients and water as a mechanism for the suppression of regenerating trees is inconsistent with the available evidence. However, the evidence presented in this study implicating allelopathy is only rudimentary and has not been tested as rigorously as some alternative hypotheses.

Woods *et al.* (1959) and Willard and McKell (1973) have demonstrated that the root starch reserves of trees can be depleted by the regular removal of above-ground parts. Furthermore the death of savanna plants following burning has been attributed to the depletion of root carbohydrate stores (Miyanishi and Kellman 1986). This evidence provides an explanation for the mechanics of growth supression that has been presented in this thesis. It may be that the growth of woody sprouts is limited by the availability of underground starch reserves. The accumulation of starch reserves in lignotubers and root systems

may be limited because stem growth is inhibited by the external influences discussed above. The necessity to develop stores of carbohydrate in the root system before dynamic shoots can be initiated may help to explain why there is a delay between fire relief or overstorey removal and the development of woody sprouts as saplings. Chapter 3 monitored the growth of woody sprouts over two fire free years but demonstrated little development of saplings, although clearly saplings can develop after long fire free periods (Chapter 4). A similar comparison can be made between the short (section 5.3.3) and longerm (section 5.3.4) effects of overstorey removal.

8.2 The regeneration process

Fig. 8.1 synthesizes some of the ideas and findings presented in the previous section and uses them to suggest the regeneration process of *Eucalyptus miniata*. Germination and sapling development occur sporadically and the influences determining their occurrence were difficult to decipher in the time frame of this study. Consequently some features of the process can only be surmised from the available evidence.

Many ecologists have noted that tree seedlings are rarely observed in the tropical eucalypt forest. The reproductive phenology of tropical trees was not formally examined during this study. However, the collection of *Eucalyptus miniata* and *Eucalyptus tetrodonta* seed for the experimental components of this study was a tedious task. Individual trees of these species were inspected using binoculars when capsules were ripe in August. In order to find one tree worthy of harvest many hundreds of trees without fruit were examined. The paucity of mature fruit on the dominant evergreen eucalypts may represent intrinsic phenological phenomena or may result from harvesting of flowers and young fruits by arboreal animals. Seedlings of the evergreen forest eucalypts were always observed under adult trees that had successfully set fruit. These observations suggest that the rarity of eucalypt seedlings is a function of a meagre seed rain. The probable long life of woody sprouts means that seedlings only have to occur sporadically to ensure the ground layer stratum of the tree population is maintained.

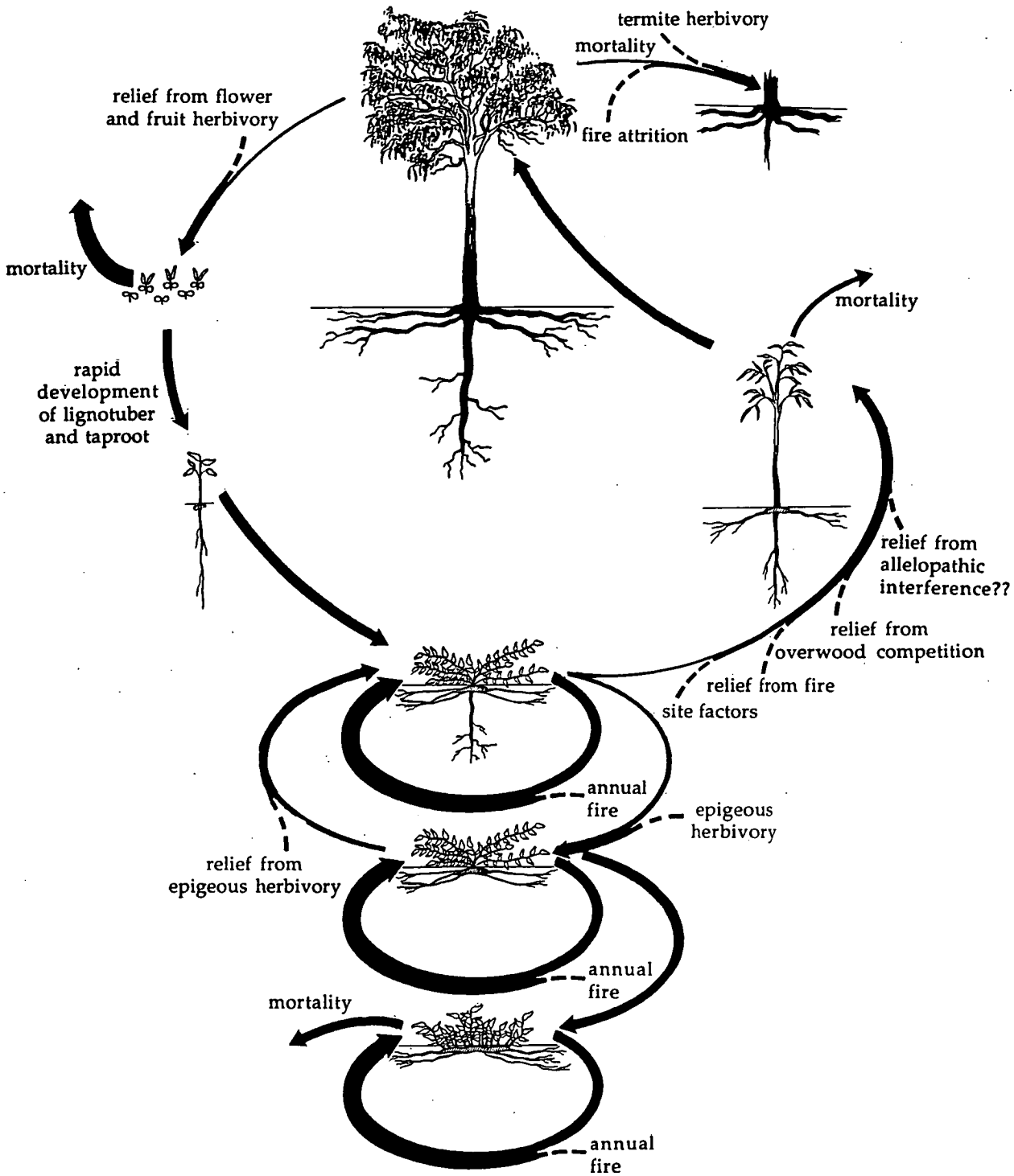


Figure 8.1 The suggested regeneration cycle of *Eucalyptus miniata*. Solid lines follow the pathways of development and degeneration, and broken lines indicate the influences on this process. The thickness of the lines gives a relative indication of the probability of each step occurring.

Soon after germination the established seedlings rapidly develop a lignotuber and a deep root system. The above-ground stems are usually incinerated within 6 months of germination and new stems regenerate from the young lignotuber. There is rapid development of a morphology and phenology that resembles older individuals in the ground layer (Chapter 7). The vast majority of lignotubreous stems remain dormant through the wet season when moisture conditions appear to be optimal. By the fire season of the following year, most woody sprouts are decrepit and many stems die. The annual cycle of regeneration and degeneration of plagiotropic lignotuberous stems will occur regardless of fire (Chapter 3). However, fire does manifest the process because all stems are destroyed and a mass of new stems emerge from the blackened earth. The accession of stems that are physiologically capable of becoming saplings is favoured by fire protection in certain environments (Chapter 4).

In order to access sufficient resources to produce sapling size stems, the underground organs of lignotuberous trees need to be well developed. It appears that there is an optimum lignotuber age from which tree stems will grow. Lignotubers will not produce saplings until they have developed an extensive root system. Furthermore, saplings are not produced by large, old lignotubers because resources are shared between numerous buds and the chances of producing a single successful stem declines (Chapter 6).

The roots of trees are readily consumed by termites (Chapter 6) and it is suggested that the avoidance of underground herbivory is an important determinant of root development and consequently sapling success. The opportunities for regeneration are enhanced when the death of an overstorey tree provides relief from competition or other interference (Chapter 6).

The time frames for most of the stages in the regeneration cycle are not clearly known. Chapter 7 documents the development of a lignotuber within 12 months after germination. The lifespan of lignotubers is totally unknown. Eucalypt lignotubers from southern New South Wales have been radiocarbon dated to 600 years (Head and Lacey 1988).

While lignotubers in the tropics would have a much shorter life because of termite attack their lifespan may be considerable.

Once sapling shoots are initiated they grow rapidly. An individual was recorded growing 4 m in height in 12 months and stems up to 28 cm diameter were recorded in 13 year old regeneration on Karslake Peninsula (Chapter 6).

Tree rings are difficult to read for the eucalypts of the seasonal tropics (Mucha 1979) and their have been disparate estimates of tree ages from northern Australia. Mucha (1979) used historical and dendrochronological evidence to conclude that trees rarely live to 100 years in the tropical eucalypt forest. Werner (1986) extrapolated from measurements over 2 years of incremental increase in the girth of tropical eucalypts and concluded that large trees may be between 150 and 400 years.

The generalized regeneration process suggested for *Eucalyptus miniata* (Fig. 8.1) has some relevance to most tree species in the tropical eucalypt forest. However, some of the important differences between the regeneration of this species and other common tree species can be noted. Fruit production is limited in eucalypts compared to other common tree species. Broadleaved species such as *Buchanania obovata, Planchonia careya* and *Terminalia ferdinandiana* will set fruit on annual stems in the ground layer. Species such as *Eucalyptus tetrodonta* and many *Acacia* species are capable of vegetative spread. The extent to which these species actually regenerate tree sized stems by this method is uncertain. However, it is known to occur and provides an alternative system to the one described above. The life stages from sapling to tree are rarely evident for broadleaved tree species in forest dominated by evergreen eucalypts.

There are no descriptions in the literature of a regeneration system matching that presented in Fig. 8.1. However, the regeneration process described in this study may have relevance in other continents. Many features of the morphology and growth phenology of the trees described in this study are shared by the trees of other tropical savanna (eg. Sarmiento and Monasterio 1983).

The regeneration model described here could be further tested by determining the factors controlling the physiological condition of woody sprouts in the ground layer of the tropical eucalypt forest. Further investigations of the mechanism of overwood suppression are also needed.

REFERENCES

ABBOTT, I. & LONERAGAN, 0. 1984. Growth rate and long-term population dynamics of jarrah (*Eucalyptus marginata* Don ex Sm.) regeneration in Western Australian forest. *Australian Journal of Botany* 32:353-362.

ALDRICK, J. M. 1976. Soils of the Alligator Rivers area. Pp. 71-88 in *Lands of the Alligator Rivers area, Northern Territory.* CSIRO Australian Land Research Series No. 38. CSIRO.

AL-MOUSAWI, A. H. & AL-NAIB, F. A. G. 1975. Allelopathic effect of *Eucalyptus microtheca* F. Muell. *University of Kuwait (Science) Bulletin* 2:59-66.

ALVIM, P. DE T. 1964. Tree growth periodicity in tropical climates. Pp. 479-495 in Zimmermann, M. H. (ed.). *Formation of wood in forest trees.* Academic Press.

ALVIM, P. DE T. & ALVIM, R. 1978. Relation of climate to growth periodicity in tropical trees. Pp. 445-464 in Tomlinson, P. B. & Zimmerman, M. H. (eds). *Tropical trees as living systems.* Cambridge University Press.

ANDERSEN, A. N. & LONSDALE, W. M. 1990. Herbivory by insects in Australian tropical savannas: A review. *Journal of Biogeography* 17:433-444.

ANDERSEN, D. C. 1987. Below-ground herbivory in natural communities: A review emphasizing fossorial animals. *The Quaterly Review of Biology* 62:261-286.

ANDREW, M. H. 1986. Population dynamics of the tropical annual grass *Sorghum intrans* in relation to local patchiness in abundance. *Australian Journal of Ecology* 11:209-218.

ANONYMOUS. 1983. *The tiwi calender.* Nguiu Nginingawila Literature Production Centre.

ANPWS. 1980. *Kakadu National Park plan of management.* Australian National Parks and Wildlife Service.

ASHTON, D. H. 1981. Fire in tall open forests (wet sclerophyll forests) Pp. 339-366 in Gill, A. M., Groves, R. H. & Noble, I. R. (eds). *Fire and the Australian biota.* Australian Academy of Science.

ASHTON, D. H. & WILLIS, E. J. 1982. Antagonisms in the regeneration of *Eucalyptus regnans* in the mature forest. Pp. 113-128 in Newman, E. I. (ed.). *The plant community as a working mechanism.* British Ecological Society.

BAZZAZ, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10:351-371.

BELL, A. 1981. Fire damages top-end forests. *Ecos* 30:18-20.

BELSKY, A. J. 1990. Tree/grass ratios in East African savanna: a comparison of existing models. *Journal of Biogeography* 17:483-489.

BENTLEY, S. & WHITTAKER, J. B. 1979. Effects of grazing by a Chrysomelid beetle, *Gasotrphysa viridula,* on competition between *Rumex obtusifoilius* and *Rumex crispus. Journal of Ecology* 67:79-90.

BEVEGE, D. I. 1968. Inhibition of seedling hoop pine (*Araucaria cunninghamii* Ait.) on forest soils by phytotoxic substances from the root zones of *Pinus, Araucaria,* and *Flindersia. Plant and Soil* 29:263-273.

BIGGER, M. 1976. Oscillations of tropical insect populations. *Nature* 259:207-209.

BLAINEY, G. 1975. *Triumph of the nomads: a history of ancient Australia.* Sun Books.

BLASCO, F. 1983. The transition from open forest to savanna in continental southeast Asia. Pp. 167-182 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas*. Elsevier Science Publishing Company.

BLYDENSTEIN, J. 1967. Tropical savanna vegetation of the Llanos of Colombia. *Ecology* 48:1-15.

BOALER, S. B. 1963. The annual cycle of stem growth increment in trees of *Pterocarpus angolensis* DC., at Kabungu, Tanganyika. *Commonwealth Forestry Review* 42:232-236.

BORCHERT, R. 1973. Simulation of rhythmic tree growth under constant conditions. *Physiologia Plantarum* 29:173-180.

BORCHERT, R. 1978. Feedback control and age-related changes of shoot growth in seasonal and nonseasonal climates Pp. 497-515 in Tomlinson, P. B. & Zimmerman, M. H. (eds). *Tropical trees as l;iving systems*. Cambridge University Press.

BOURLIERE, F. & HADLEY, M. 1983. Present-day savannas: an overview. Pp. 1-18 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas*. Elsevier Science Publishing Company.

BOWMAN, D. M. J. S. 1986. Stand characteristics, understorey associates and environmental correlates of *Eucalyptus tetrodonta* F. Muell. forests on Gunn Point, Northern Australia. *Vegetatio* 65:105-113.

BOWMAN, D. M. J. S. 1988. Stability amid turmoil?: towards an ecology of north Australian eucalypt forests. *Proceedings of the Ecological Society of Australia* 15:149-158.

BOWMAN, D. M. J. S. & DUNLOP, C. R. 1986. Vegetation patterns and environmental correlates in coastal forests of the Australian monsoon tropics. *Vegetatio* 65:99-104.

BOWMAN, D. M. J. S. & KIRKPATRICK, J. B. 1986a. The establishment, suppression and growth of *Eucalyptus delegatensis* R. T. Baker in multi aged forests. II. Sapling growth and its environmental correlates. *Australian Journal of Botany* 34:73-80.

BOWMAN, D. M. J. S. & KIRKPATRICK, J. B. 1986b. The establishment, suppression and growth of *Eucalyptus delegatensis* R. T. Baker in multi aged forests. III. Intraspecific allelopathy, competition between adult and juvenile for moisture and nutrients, and frost damage to seedlings. *Australian Journal of Botany* 34:81-94.

BOWMAN, D. M. J. S., & MINCHIN, P. R. 1987. Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. *Australian Journal of Botany* 35:151-169.

BOWMAN, D. M. J. S. & WILSON, B. A. 1988. Fuel characteristics of coastal monsoon forests, Northern Territory, Australia. *Journal of Biogeography* 15:807-817.

BOWMAN, D. M. J. S., WILSON, B. A. & DAVIS, G. W. 1988a. Response of *Callitris intratropica* R. T. Baker & H. G. Smith to fire protection, Murgenella, northern Australia. *Aust.ralian Journal of Ecology*. 13:147-159.

BOWMAN, D. M. J. S., WILSON, B. A. & DUNLOP, C. R. 1988b. Preliminary biogeographic analysis of the Northern Territory vascular flora. *Australian Journal of Botany* 36:503-517.

BOWMAN, D. M. J. S., WILSON, B. A. & HOOPER, R. J. 1988c. Response of *Eucalyptus* forest and woodland to four fire regimes at Munmalary, Northern Territory, Australia. *Journal of Ecology*. 76:215-232.

BOWMAN, D. M. J. S., WILSON, B. A. & WOINARSKI, J. C. Z. 1990. Floristic and phenological variation in a northern Australian rocky *Eucalyptus* savanna. *Proceedings of the Royal Society of Queensland*. 101 (in press).

BRAITHWAITE, R. W. & ESTBERGS, J. A. 1985. Fire patterns and woody vegetation trends in the Alligator Rivers region of Northern Australia. Pp. 309-322 in Tothill, J. C. & Mott, J. J. (eds). *Ecology and management of the world's savannas.* Australian Academy of Science.

BRAITHWAITE, R. W., MILLER, L. & WOOD, J. T. 1988. The structure of termite communities in the Australian tropics. *Australian Journal of Ecology* 13:375-391.

BREEN, J. P. & TEESTES, G. L. 1986. Relationships of yellow sugarcane aphid (Homoptera: Aphididae) density to sorghum damage. *Journal of Economic Entomology* 79:1106-1110.

BROKAW, N. V. L. 1985. Treefalls, regrowth and community structure in tropical forests. Pp. 53-71 in Pickett, S. T. A. & White, P. S. (eds). *The Ecology of natural disturbance and patch dynamics* Academic Press.

BROKAW, N. V. L. & SCHEINER, S. M. 1989. Species composition in gaps and structure of a tropical forest. *Ecology* 70:538-541.

BROWN, V. K. 1984. Secondary succession: insect-plant relationships. *Bioscience.* 34(11):710-716.

BROWN, M. J., RATKOWSKY, D. A. & MINCHIN, P. R. 1984. A comparison of detrended correspondence analysis and principal co-ordinates analysis using four sets of Tasmanian vegetation data. *Australian Journal of Ecology.* 9:273-279.

BROWN, V. K. & GANGE, A. C. 1989. Differential effects of above- and below-ground insect herbivory during early plant succession. *Oikos.* 54:67-76.

BUCHANAN, F. 1807. *A journey from Madras through the countries of Mysore, Kanara and Malabar.* 3 volumes. East India Company.

BUDYKO, M. I. 1974. *Climate and life.* Academic Press.

BURDON, J. J. & CHILVERS, G. A. 1974a. Fungal and insect parasites contributing to niche differentiation in mixed species stands of eucalypt saplings. *Australian Journal of Botany* 22:103-114.

BURDON, J. J. & CHILVERS, G. A. 1974b. Leaf parasites on altitudinal populations of *Eucalyptus pauciflora* Sieb. ex Spreng. *Australian Journal of Botany* 22:265-269.

BUREAU OF METEOROLOGY. 1988. *Climatic averages Australia.* Australian Government Publishing Service.

BUTLER, B. E. 1955. A system for the description of soil structure and consistence in the field. *Journal of the Australian Institute of Agricultural Science* 21:239-249.

CALDER, G. J. & DAY, K. J. 1982. *Fertility studies on four soils of the northen lateritic uplands, Northern Territory.* Technical Bulletin. 48. Northern Territory Department of Primary Industries.

CANTOR, L. F. & WHITHAM, T. G. 1989. Importance of belowground herbivory: Pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70:962-970.

CARR, S. G. M. 1972. Problems of the geography of the tropical eucalypts. Pp. 153-182 in Walker, D. J. (ed). *Bridge and Barrier: the natural and cultural history of Torres Strait.* Australian National University Publication BG/3.

CARR, D. J., JAHNKE, R. & CARR, S. G. M. 1984. Initiation, development and anatomy of lignotubers in some species o *Eucalyptus. Australian Journal of Botany* 32:415-437.

CARRODUS, B. B. & BLAKE, T. J. 1970. Studies on the lignotubers of *Eucalyptus obliqua* L'Herit. I The nature of the lignotuber. *New Phytologist* 69:1069-1072.

CHILVERS, G. A. & BRITTAIN, E. G. 1972. Plant competition mediated by host-specific parasites- a simple model. *Australian Journal of Biological Science* 25:749-756.

CHRISTENSEN, P., RECHER, H. & HOARE, J. 1981. Responses of open forests to fire regimes. Pp. 367-394 in Gill, A. M., Groves, R. H. & Noble, I. R. (eds). *Fire and the Australian biota*. Australian Academy of Science.

CHU-CHOU, M. 1978. Effects of root residues on growth of *Pinus radiata* seedlings and a mycorrhizal fungus. *Annals of Applied Biology* 90:407-416.

CLEMENTS, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institute of Washington Publication No. 242.

COLE, M. M. 1960. Cerrado, caatinga and Pantanal: The distribution and origin of the savanna vegetation of Brazil. *Geographical Journal* 126:168-179.

COLEY, P. D. 1980. Effects of leaf age and plant life history patterns on herbivory. *Nature* 284:545-546.

COLEY, P. D. 1983. Intraspecific variation in herbivory on two tropical tree species. *Ecology* 64:426-433.

COUTHINO, L. M. 1982. Ecological effects of fire in Brazilian *cerrado*. Pp. 273-291 in Huntley, B. J. & Walker, B. H. (eds). *Ecological studies 42: ecology of tropical savannas* Springer-Verlag.

COVENTRY, R. J. & FETT, D. E. R. 1979. *A pipette and sieve method of particle size analysis and some observations on its efficacy*. Technical Memorandum 38. Division of Soils, CSIRO.

CRAWLEY, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Pp. 45-71 in Bernays, E. A. (ed.). *Insect-plant interactions*. CRC Press.

CSIRO, 1970. *The insects of Australia.* Melbourne University Press, Carlton, Victoria.

CSIRO, 1982. *Notes on soil techniques. No. 4.* CSIRO, Division Soils, Canberra.

CULLEN, P. J. 1987. Regeneration patterns in populations of *Arthrotaxis selaginoides* D. Don. from Tasmania. *Journal of Biogeography* 14:39-51.

CURTIS, L. F. & TRUDGILL, S. 1974. *The measurement of soil moisture.* Technical Bulletin 13. British Geomorphology Research Group.

DALE, D. 1989. Plant-mediated effects of soil mineral stresses on insects. Pp. 35-110 in Heinrichs, E. A. (ed.). *Plant stress-insect interactions.* John Wiley and Sons.

DAUBENMIRE, R. F. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *Journal of Ecology.* 60:147-170.

DAVIS, S. 1989. *Man of all seasons* Angus and Robertson.

DAY. K. J. 1977. *Fertility studies on three red earth soils of the Daly Basin, Northern Territory.* Technical Bulletin 22. Department of the Northern Territory Animal Industry and Agriculture Branch.

DEL MORAL, R. & MULLER, C. H. 1969. Fog drip: a mechanism of toxin transport from *Eucalyptus globulus. Bulletin of the Torrey Botanical Club* 96:467-475.

DEL MORAL, R. & MULLER, C. H. 1970. The allelopathic effects of *Eucalyptus camadulensis. American Midland Naturalist* 83:254-282.

DEL MORAL, R., WILLIS, R. J. & ASHTON, D. H. 1978. Suppression of coastal heath vegetation by *Eucalyptus baxteri*. *Australian Journal of Botany* 26:203-219.

DUNLOP, C. R. 1987. *Checklist of vascular plants of the Northern Territory*. Technical Report 26. Conservation Commission of the Northern Territory.

DUNLOP, C. R. 1988. Eucalypt communities Pp. 13-17 in Brock, J. (ed.). *Top End native plants*. John Brock.

DUNN, A. J. & MEHUYS, G. R. 1984. Relationship between gravel content of soils and saturated hydraulic conductivity in labratory tests. Pp. 55-63 in Kral, D. M. (ed.). *Erosion and productivity of soils containing rock fragments*. Soil Science Society of America. Special publication no. 13.

EDEN, M. J. 1964. *The savanna ecosystem- Northern Rupununi, British Guiana*. Savanna Research Series No. 1. McGill University Savanna Research Project.

EDWARDS, W. M., GERMANN, P. F., OWENS, L. B. & AMERMAN, C. R. 1984. Watershed studies of factors influencing infiltration, runoff, and erosion on stony and non-stony soils. Pp. 45-54 in Kral, D. M. (ed.). *Erosion and productivity of soils containing rock fragments*. Soil Science Society of America. Special publication no. 13.

EITEN, G. 1972. The *cerrado* vegetation of Brazil. *Botanical Review*. 38:201-341.

EITEN, G. 1975. The vegetation of the Serra do Roncador. *Biotropica*. 7:112-135.

ELLIS, R. C., RATKOWSY, D. A., MATTAY, J. P. & ROUT, A. F. 1987. Growth of *Eucalyptus delegatensis* following partial harvesting of multi-aged stands. *Australian Forestry* 50:95-105.

EVANS, G., CARTWRIGHT, J. B. & WHITE, N. H. 1967. The production of a phytotoxin, nectrolide, by some root-surface isolates of *Cylindrocarpon radicola*, Wr. *Plant and Soil* 26:253-260.

FERRAR, P. J., SLATYER, R. O. & VRANJIC, J. A. 1989. Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitats, and a comparison with *Nerium oleander*. *Australian Journal of Plant Physiology*. 16:199-217.

FLORENCE, R. G. & CROCKER. L. 1962. Analysis of blackbutt (*Eucalyptus pilularis* Sm.) seedling growth in a blackbutt forest soil. *Ecology* 43:670-679.

FOLDATS, E. & RUTKIS, E. 1975. Ecological studies of chaparro (*Curatella americana* L.) and manteco (*Byrsonima crassifolia* H.B.K.) in Venezuela. *Journal of Biogeography* 2:159-178.

FOX, L. R. & MORROW, P. A. 1983. Estimates of damage by insect grazing on *Eucalyptus* trees. *Australian Journal of Ecology* 8:439-447.

FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881-919.

FRITH, C. B. & FRITH, D. W. 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* 10:237-248.

GAUCH, H. G. & WHITTAKER, R. H. 1981. Hierachical classification of community data. *Journal of Ecology*. 69:135-152.

GIBSON, C. W. D., BROWN, V. K. & JEPSEN, M. 1987. Relationships between the effects of insect herbivory and sheep grazing on seasonal changes in an early successional plant community. *Oecologia*. 71:245-253.

GILL, A. M. 1981. Adaptive responses of Australian vascular plant species to fires. Pp. 243-272 in Gill, A. M., Groves, R. H. & Noble, I. R. (eds). *Fire and the Australian biota*. Australian Academy of Science.

GILLISON, A. N. 1983. Tropical savannas of Australia and the southwest Pacific. Pp. 183-244 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas*. Elsevier Science Publishing Company.

GILLON, D. 1983. The fire problem in the tropical savannas. Pp. 617-642 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas*. Elsevier Science Publishing Company.

GILLON, Y. 1983. The invertebrates of the grass layer. Pp. 289-312 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas.* Elsevier Science Publishing Company.

GOLDSTEIN, G. & SARMIENTO, G. 1987. Water relations of trees and grasses and their consequences for the structure of savanna vegetation. Pp. 13-38 in Walker, B. H. (ed.). *Determinants of tropical savannas.* IRL Press.

GOODALE, J. C. 1971. *Tiwi wives.* University of Washington Press.

GREATHOUSE, D. C., LAETSCH, W. M., & PHINNEY, B. O. 1971. The shoot growth rhythm of a tropical tree, *Theobroma cacao. American Journal of Botany* 58:281-286.

GREAVES, R. 1966. Insect defoliation of eucalypt regrowth in the Florentine Valley, Tasmania. *Australian Forestry Research* 3:36-45.

GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review of the Cambridge Philosophical Society* 52:107-145.

GUPTA, S. C. & LARSON, W. E. 1979. Estimating soil water retention characterisitcs from particle size distribution, organic matter percent and bulk density. *Water Resource Research* 15:1633-1635.

HALLAM, S. S. 1975. *Fire and hearth.* Australian Institute of Aboriginal Studies.

HARRIS, P. 1974. A possible explaination of plant yield increases following insect damage. *Agro-ecosystems* 1:219-225.

HART, C. W. M. & PILLING, A. R. 1960. *The Tiwi of north Australia.* Holt, Rhinehart and Winston.

HAYNES, C. D. 1985. The pattern and ecology of *munwag*: traditional aboriginal fire regimes in north-central Arnhemland. *Proceedings of the Ecological Society of Australia* 13:203-214.

HEAD, M. J. & LACEY, C. J. 1988. Radiocarbon age determinations from lignotubers. *Australian Journal of Botany* 36:93-100.

HENRY, N. B. & FLORENCE, R. G. 1966. Establishment and development of regeneration in spotted gum-ironbark forests. *Australian Forestry* 30:304-316.

HETT, J. M. & LOUCKS, O. L. 1976. Age structure models of balsam fir and eastern hemlock. *Journal of Ecology* 64:1029-1044.

HILL, M. O 1979a. *DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Ecology and Systematics, Cornell University, Ithica, New York.

HILL, M. O. 1979b. *TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Ecology and Systematics, Cornell University, Ithica, New York.

HILLEL, D. 1971. *Soil and water*. Academic Press.

HODGKINSON, K. C. & GRIFFIN, G. F. 1982. Adaptation of shrub species to fires in the arid zone. Pp. 145-152 in Barker, W. R. & Greenslade, P. J. M. (eds). *Evolution of the flora and fauna of arid Australia*. Peacock Publications.

HODKINSON, I. D. & CASSON, D. S. 1987. A survey of food-plant utilization by Hemiptera (Insecta) in the understorey of primary lowland rainforest in Sulawesi, Indonesia. *Journal of Tropical Ecology* 3:75-85.

HODKINSON, I. D. & HUGHES, M. K. 1982. *Insect herbivory*. Chapman & Hall.

HOLTZER, T. O., ARCHER, T. L. & NORMAN, J. M. 1989. Host plant suitability in relation to water stress. Pp. 111-138 in Heinrichs, E. A. (ed.). *Plant stress-insect interactions*. John Wiley and Sons.

HOPKINS, B. 1963. The role of fire in promoting the sprouting of some savanna species. *Journal of the West African Science Association* 7:154-162.

HOPKINS, B. 1970a. Vegetation of the Olokemeji Forest Reserve, Nigeria. VI. The plants on the forest site with special reference to their seasonal growth. *Journal of Ecology*.58:765-793.

HOPKINS, B. 1970b. Vegetation of the Olokemeji Forest Reserve, Nigeria. VII. The plants on the savanna site with special reference to their seasonal growth. *Journal of Ecology* 58:795-825.

HUGHES, R. J. 1976. *Bathurst and Melville Island SC/52-15 and SC/52-16 1:250 000 geological map Series explanatory notes.* Northern Territory Geological Survey.

HUXLEY, P. A. & VAN ECK, W. A. 1974. Seasonal changes in growth and development of some woody perennials near Kampala, Uganda. *Journal of Ecology* 62:579-592.

INCOLL, W. D. 1979. Effect of overwood trees on growth of young stands of *Eucalyptus sieberi*. *Australian Forestry* 42:110-116.

ISBELL, R. F., JONES, R. K. & GILLMAN, G. P. 1976. Plant nutrition studies on some yellow and red earth soils in northern Cape York Peninsula. 1. Soils and their nutrient status. *Australian Journal of Experimental Agriculture and Animal Husbandry* 16:532-541.

ISBELL, R. F. & SMITH, G. M. 1976. *Some properties of red, yellow and grey massive earths in North Queensland, Australia.* Technical Paper. 30. Division of Soils, CSIRO.

JACOBS, M. T. 1955. *Growth habits of the eucalypts.* Forestry and Timber Bureau, Canberra.

JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day and insularity. *Ecology* 54:687-701.

JANZEN, D. H. & SCHOENER, T. W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49:96-110.

JEFFERS, J. N. R. & BOALER, S. B. 1966. Ecology of a *miombo* site, Lupa North Forest Reserve, Tanzania. I. Weather and plant growth, 1962-64. *Journal of Ecology* 54:447-463.

JONES, R. 1980. Hunters in the Australian coastal savanna. Pp. 107-146 in Harris, D. (ed.). *Human ecology in savanna environments.* Acacdemic Press.

JOSENS, G. 1983. The fauna of tropical savannas. III. The termites. Pp. 505-524 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas.* Elsevier Science Publishing Company.

JOURNET, A. R. P. 1981. Insect herbivory on the Australian woodland eucalypt, *Eucalyptus blakelyi.* M. *Australian Journal of Ecology* 6:135-138.

JUO, A. S. R., AYANLAJA, S. A. & OEUNWALE, J. A. 1976. An evaluation of cation exchange capacity measurements for soils in the tropics. *Communications in Soil Science and Plant Analysis* 7:751-761.

KEENAN, T. D., MORTON, B. R., ZHANG, X. S. & NGUYEN, K. 1989. Some characteristics of thunderstorms over Bathurst and Melville Islands near Darwin, Australia. *Quaterly Journal of the Royal Meteorological Society* 116:1153-1172.

KELLMAN, M. 1979. Soil enrichment by neotropical savanna trees. *Journal of Ecology* 67:565-577.

KELLMAN, M. 1985. Forest seedling establishment in neotropical savannas: transplant experiments with *Xylopia frutescens* and *Calophyllum brasiliense*. *Journal of Biogeogrphy* 12:373-379.

KELLMAN, M. & MIYANISHI, K 1982. Forest seedling establishment in neotropical savannas: observations and experiments in the Mountain Pine Ridge, Belize. *Journal of Biogeography* 9:193-206.

KERLE, J. A. 1985. Habitat preference and diet of the northern brushtail possum *Trichosurus arnhemensis* in the Alligator Rivers region, N. T. *Proceedings of the Ecological Society of Australia* 13:161-175.

KILE, G. A. 1974. Insect defoliation in the eucalypt regrowth forests of southern Tasmania. *Australian Forest research* 6:9-18.

KIMBER, R. G. 1983. Black Lightning: Aborigines and Fire in Central Australia and the Western Desert. *Archaeology in Oceania* 18:38-45.

KIRKPATRICK, J. B., BOWMAN, D. M. J. S., WILSON, B. A. & DICKINSON, K. J. M. 1987. A transect study of the *Eucalptus* forests and woodlands of a dissected sandstone plateau near Darwin, Northern Territory. *Australian Journal of Ecology*. 12:339-359.

KIRKPATRICK, J. B., FENSHAM, R. J., NUNEZ, M. & BOWMAN, D. M. J. S. 1988. Vegetation-radiation relationships in the wet-dry tropics: granite hills in northern Australia. *Vegetatio* 76:103-112.

KNOOP, W. T. & WALKER, B. H. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73:235-253.

KULMAN, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology* 16:289-324.

LACEY, C. J. 1974. Rhizomes in tropical eucalypts and their role in recovery from fire damage. *Australian Journal of Ecology* 22:29-38.

LACEY, C. J. & JOHNSTON, R. D. 1990. Woody clumps and clumpwoods. *Australian Journal of Botany* 38:299-334.

LACEY, C. J., WALKER, J. & NOBLE, I. R. 1982. Fire in Australian tropical savannas. Pp. 246-272 in Huntley, B. J. & Walker, B. H. (eds). *Ecological studies 42: ecology of tropical savannas* Springer-Verlag.

LACEY, C. J. & WHELAN, P. I. 1976. Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Australian Forestry* 39:131-139.

LANDSBERG, J. 1989. A comparison of methods for assessing defoliation, tested on eucalypt trees. *Australian Journal of Ecology* 14:423-440.

LANDSBERG, J. 1990. Dieback of rual eucalypts: does insect herbivory relate to dietary quality of tree foliage? *Australian Journal of Ecology* 15:73-87.

LANDSBERG, J. & WYLIE, F. R. 1983. Water stress, leaf nutrients and defoliation: a model of dieback caused by leaf feeding insects. *Australian Journal of Ecology* 8:27-41.

LANGKAMP, P. J., ASHTON, D. H. & DALLING, M. J. 1981. Ecological gradients in forest communities on Groote Eylandt, Northern Territory, Australia. *Vegetatio* 48:27-46.

LILL, R. E. & WAID, J. S. 1975. Volatile phytotoxic substances formed by litter of *Pinus radiata*. *New Zealand Journal of Forest Science* 5:61-63.

LOCKETT, E. J. & CANDY, S. G. 1984. Growth of eucalypt regeneration established with and without slash burns in Tasmania. *Australian Forestry* 47:119-125.

LONGMAN, K. A. 1978. Control of shoot extension and dormancy: external and internal factors. Pp. 465-495 in Tomlinson, P. B. & Zimmerman, M. H. (eds). *Tropical trees as living systems*. Cambridge University Press.

LOPES, A. S. & COX, F. R. 1977. Cerrado vegetation in Brazil: an edaphic gradient. *Agricultural Journal* 69:828-831.

LORIMER, C. G. 1983. Eighty-year development of northern red oak after partial cutting in a mixed-species Wisconsin forest. *Forest Science* 29:371-383.

LOWMAN, M. D. 1982. Seasonal variation in insect abundance among three Australian rainforests, with particular reference to phytophagous types. *Australian Journal of Ecology* 4:353-362.

LOWMAN, M. D. 1984. An assessment of techniques for measuring herbivory:is rainforest defoliation more intense than we thought? *Biotropica* 16:264-268.

LOWMAN, M. D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* 10:7-24.

LOWMAN, M. D. 1987. Relationships between leaf growth and holes caused by herbivores. *Australian Journal of Ecology* 12:189-191.

LOWMAN, M. D. & HEATWOLE, H. 1987. The impact of defoliating insects on the growth of eucalypt saplings. *Australian Journal of Ecology* 12:175-181.

LOWMAN, M. D., BURGESS, A. D. & HIGGINS, W. D. 1987. The biomass of New England peppermint (*Eucalyptus nova-anglica*) in relation to insect damage associated with rural dieback. *Australian Journal of Ecology* 12:361-372.

MCALPINE, J. R. 1976. Climate and water balance. Pp. 35-49 in *Lands of the Alligator Rivers area, Northern Territory*. CSIRO Australian Land Research Series No. 38. CSIRO.

MCDONALD, P. M. 1976. Inhibiting effect of ponderosa pine seed trees on seedling growth. *Journal of Forestry* 74:220-224.

MCDONALD, R. C., ISBELL, R. F., SPEIGHT, J. G., WALKER, J. & HOPKINS, M. S. 1984. *Australian soil and land survey*. Inkata Press.

MCINTYRE, D. S. 1974. Water retention and moisture characteristics. Pp. 43-62 in Loveday, J. *Methods for analysis of irrigated soils*. Technical Communication 54. Commonwealth Agricultural Bureaux.

MAGDUF, P. & GARTI, R. 1971. *Guidelines for soil reclaimation*. (in Hebrew). Report 30. Soil Conservation and Drainage Division, Ministry of Agriculture, Israel.

MAGIER, J. & RAVINA, I. 1984. Rock fragments and soil depth as factors in land evaluation of terra rossa. Pp. 13-30 in Kral, D. M. (ed.).*Erosion and productivity of soils containing rock fragments*. Soil Science Society of America. Special publication no. 13.

MATTSON, W. J. & ADDY, N. D. 1975. Phytophagous insects as regulators of primary production. *Science* 190:515-522.

MAY, F. E. & ASH, J. E. 1990. An assessment of the allelopathic potential of *Eucalyptus*. *Australian Journal of Botany* 38:245-254.

MAYER, A. M. & POLJAKOFF-MAYBER, A. 1982. *The germination of seeds*. Third Edition. Pergamon Press.

MEDINA, E. 1982. Physiological ecology of neotropical savanna plants. Pp. 308-335 in Huntley, B. J. & Walker, B. H. (eds). *Ecological studies 42: ecology of tropical savannas* Springer-Verlag.

MEDINA, E. & SILVA, J. F. 1990. Savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. *Journal of Biogeography* 17:403-413.

MESSEL, H., WELLS, A. G. & GREEN, W. J. 1979. *Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations: Monograph 6 some river and creek systems on Melville and Grant Islands*. Pergamon Press.

MINCHIN, P. R. 1986. *How to use ECOPAK: an ecological database system*. Technical Memorandum 86/6. Division of Water and Land Resources, CSIRO .

MINCHIN, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89-107.

MIYANISHI, K. & KELLMAN, M. 1986. The role of root nutrient reserves in the regrowth of two savanna shrubs. *Canadian Journal of Botany* 64:1244-1248.

MONASTERIO, M. & SARMIENTO, G. 1976. Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest of the Venezualan Llanos. *Journal of Biogeography* 3:325-356.

MORRILL, W. L., DITTERLINE, R. L. & WINSTEAD, C. 1984. Effects of *Lygus borealis* Kelton (Hemiptera: Miridae) and *Adelphocorus lineolatus* (Goeze) (Hemiptera: Miridae) feeding on sainfoin production. *Journal of Economic Entomology* 77:966-968.

MORROW, P. A. 1977a. The significance of phytophagous insects in the *Eucalyptus* forests of Australia. Pp. 19-29 in Mattson, W. J. (ed.). *The Role of Arthropods in Forest Ecosystems*. Springer-Verlag, New York.

MORROW, P. A. 1977b. Host specificity of insects in a community of three co-dominant *Eucalyptus* species. *Australian Journal of Ecology* 2:89-106.

MORROW, P. A. & LE MARCHE, V. C. 1978. Tree ring evidence for chronic insect suppression of productivity in sub-alpine *Eucalyptus*. *Science* 201:1244-1246.

MUCHA, S. B. 1979. Estimation of tree ages from growth rings of eucalypts in northern Australia. *Australian Forestry* 42:13-16.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York.

MULLETTE, K. J. & BAMBER, R. K. 1978. Studies of the lignotubers of *Eucalyptus gummifera* (Gaertn. & Hochr.) III Inheritance and chemical composition. *Australian Journal of Botany* 26:23-28

NAKASHIZUKA, T. 1987. Regeneration dynamics of beech forests in Japan. *Vegetatio* 69:169-175.

NIX, H. A. 1981. The environment of *Terra Australis*. Pp. 103-133 in Keast, A. *Ecological biogeography of Australia*. W. Junk, The Hague.

NJOKU, E. 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observation on mature trees. *Journal of Ecology* 51:617-624.

NJOKU, E. 1964. Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observation on seedlings. *Journal of Ecology* 52:19-26.

ODUM, E. P. 1969. The strategy of ecosystem development. *Science* 164:262-270.

OGAWA, H., YODA, K. & KIRA, T. 1961. A preliminary survey on the vegetation of Thailand. *Nature and Life in South East Asia* 1:21-157.

OHMART, C. P., STEWART, L. G. & THOMAS, J. R. 1983a. Leaf consumption by insects in threee *Eucalyptus* forest types in southeastern Australia and their role in short-term nutrient cycling. *Oecologia* 59:322-330.

OHMART, C. P., STEWART, L. G. & THOMAS, J. R. 1983b. Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in south-eastern Australia. *Australian Journal of Ecology* 8:395-403.

OLLIER, C. D. & GALLOWAY, R. W. 1990. The laterite profile, ferricrete and uncomformity. *Catena* 17:97-109.

PARKER, A. J. 1986. Environmental and historical factors affecting red and white fir regeneration in ecotonal forests. *Forest Science* 32:339-347.

PARSONS, R. F. 1968. An introduction to the regeneration of mallee eucalypts. *Proceedings of the Royal Society of Victoria* 81:59-68.

PATON, T. R. & WILLIAMS, M. A. J. 1972. The concept of laterite. *Annals of the Association of American Geographers* 62:42-56.

PIETSCH, B. A. & STUART-SMITH, P. G. 1987. *Darwin SD52-4. 1:250 000 geological map series explanatory notes.* Northern Territory Geological Survey.

PREBBLE, R. E. 1970. *Physical properties of 17 soil groups from Queensland.* Technical Memorandum 10. Australian Division of Soils, CSIRO.

PRESS, A. J. 1988. Comparisons of the extent of fire in different land management systems in the Top End of the Northern Territory. *Proceedings of the Ecological Society of Australia* 15,167-175.

PURDIE, R. W. 1977. Early stages of regeneration after burning in dry sclerophyll vegetation. II Regeneration by seed germination. *Australian Journal of Botany* 25:35-46.

RADFORD, P. J. 1967. Growth analysis formulae- their use and abuse. *Crop Science* 7:171-175.

READ, J. S. & HILL, R. S. 1988. The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* 76:558-584.

READSHAW, J. L. & MAZANEC, Z. 1969. Use of growth rings to determine past phasmatid defoliations of alpine ash forest. *Australian Forestry* 33:29-36.

REICHLE, D. E., GOLDSTEIN, R. A., VAN HOOK, R. I. & DODSON, G. J. 1973. Analysis of insect consumption in a forest canopy. *Ecology* 54:1076-1084.

REID, D. E. 1987. *Fire and habitat modification: an anthropological inquiry into the use of fire by indigenous peoples* M. Sc. Thesis, Department of Anthropology, The University of Alberta.

REINHART, K. G. 1961. The problem of stones in soil moisture measurement. *Soil Science Society of America Proceedings* 25:268-270.

RICE, B. & WESTOBY, M. 1985. Structure of local floristic variation and how well it correlates with existing classification schemes: vegetation at Koongara, N. T. Australia. *Proceedings of the Ecological Society of Australia* 13:129-137.

RICKLEFS, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist* 111:376-381.

ROBERTSON, A. I. & DUKE, N. C. 1987. Insect herbivory on mangrove leaves in north Queensland. *Australian Journal of Ecology* 12:1-8.

ROCKWOOD, L. L. 1974. Seasonal changes in the susceptibilty of *Crescentaia alata* leaves to the flea beetle, *Oedionychus* sp. *Ecology* 55:142-148.

ROSS-INNES, R. 1972. Fire in West African vegetation. *Proceedings of the Tall Timbers Fire Ecology Conference,* 11:147-173.

ROTHERAM, I. 1983. Suppression of growth of surrounding regeneration by veteran trees of karri (*Eucalyptus diversicolor*). *Australian Forestry* 46:8-13.

RUNKLE, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533-1546.

RUSSELL, E. W. 1973. *Soil conditions and plant growth.* Longman.

RUSSELL-SMITH, J. 1986. *The forest in motion: exploratory studies in western Arnhem Land, Northern Australia.* PhD. Thesis, Australian National University.

RUSSELL-SMITH, J. & DUNLOP, C. R. 1987. Pp. 227-288 in *The rainforest legacy. Australian national rainforests study volume 1- the nature, distribution and status of rainforest types.* Australian Government Publishing Service.

SANFORD, W. W. & ISICHEI, A. O. 1986. Savanna. Pp. 95-149 in Lawson, G. W. *Plant ecology in West Africa.* John Wiley and Sons.

SAN JOSE, J. J. & FARINAS, M. R. 1983. Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuala. *Ecology* 64:447-53.

SARMIENTIO, G. 1983. The savannas of tropical America. Pp. 245-288 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas.* Elsevier Science Publishing Company.

SARMIENTO, G. 1984. *The ecology of neotropical savannas.* Harvard University Press.

SARMIENTO, G., GOLDSTEIN, G. & MEINZER, F. 1985. Adaptive strategies of woody species in neotropical savannas. *Biological Review* 60:315-355.

SARMIENTIO, G & MONASTERIO, M. 1983. Lifeforms and phenology. Pp. 79-108 in Bourliere, F. (ed.). *Ecosystems of the world 13: tropical savannas.* Elsevier Science Publishing Company.

SCHOLANDER, P. F. BRADSTREET, E. D., HAMMEL, H. T. & HEMMINGSEN, E. A. 1965. Sap pressure in vascular plants. *Science* 148:339-346.

SCHOWALTER, T. D., WEBB, J. W. & CROSSLEY, D. A. 1981. Community structure and nutrient content of canopy arthropods in clear cut and uncut forest ecosystems. *Ecology* 62:1010-1019.

SELBY, M. J. 1982. *Hillslope materials and processes*. Oxford University Press.

SILANDER, J. A., TRENBATH, B. R. AND FOX, L. R. 1983. Chemical interference among plants mediated by grazing insects. *Oecologia* 58:415-417.

SKINNER, T. C. L. 1990. *A study of the sea breeze over Melville and Bathurst Islands and its role in the development of thunderstorm activity*. B. Sc. (Hons.) thesis. Monash University.

SOKAL, R. R. & ROHLF, F. J. 1969. *Biometry*. W. H. Freeman and Co.

SPECHT, R. L. 1970. Vegetation. Pp. 44-67 in Leeper, G. W. (ed.). *The Australian environment*. CSIRO and Melbourne University Press.

SPECHT, R. L. & BROUWER, Y. M. 1975. Seasonal shoot growth of *Eucalyptus* spp. in the Brisbane area of Queensland (with notes on shoot growth and litter fall in other areas of Australia). *Australian Journal of Botany* 23:459-474.

SPECHT, R. L., SALT, R. B. & REYNOLDS, S. T. 1977. Vegetation in the vicinity of Weipa, North Queensland. *Proceedings of the Royal Society of Queensland* 88:17-38.

SPRUGEL, D. G. 1976. Dynamic structure of wave generated *Abies balsamea* forests in the northeastern United States. *Journal of Ecology* 64:889-911.

STOCKER, G. C. 1966. Effects of fires on vegetation in the Northern Territory. *Australian Forestry* 30:223-230.

STOCKER, G. C. 1971. The age of charcoal from old jungle fowl nests and vegetation change on Melville Island. *Search* 2:28-30.

STORY, R. 1976. Vegetation of the Alligator Rivers area. Pp. 89-111 in *Lands of the Alligator Rivers area, Northern Territory*. CSIRO Australian Land Research Series No. 38. CSIRO.

STOTT, P. A. 1984. The savanna forests of mainland southeast Asia: an ecological survey. *Progress in Physical Geography* 8:315-335.

STRAHLER, A. N. 1975. *Physical geography*. 4th Edition. Wiley International.

STRONG, D. R., LAWTON, J. H. & SOUTHWOOD, T. R. E. 1984. *Insects on plants: community patterns and mechanisms*. Harvard University Press.

SURESH, K. K. & VINAYA RAI, R. S. 1988. Allelopathic exclusion of understorey by a few multi-purpose trees. *The International Tree Crops Journal* 5:143-151.

TAYLOR, J. A. & DUNLOP, C. R. 1985. Plant communities of the wet-dry tropics: The Alligator Rivers region. *Proceedings of the Ecological Society of Australia* 13:83-127.

TAYLOR, J. A. & TULLOCH, D. 1985. Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870-1983. *Australian Journal of Ecology*. 10:281-295.

TEW, R. K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. *Forest Science* 16:318-320.

TOMLINSON, P.B. & GILL, A. M. 1973. Growth habits of tropical trees; some guiding principles. Pp. 129-143 in Meggers, B. J., Ayensu, E. S. & Donald, W. (eds). *Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Institution Press.

VEBLEN, T. T. 1985. Stand dynamics in Chilean *Nothofagus* forests. Pp. 35-52 in Pickett, S. T. A. & White, P. S. (eds). *The ecology of natural disturbance and patch dynamics*. Academic Press.

VEBLEN, T. T. & ASHTON, D. H. 1978. Catastrophic influences in the vegetation of the Valdivian Andes, Chile. *Vegetatio* 36:147-167.

VEBLEN, T. T., ASHTON, D. H. & SCHLEGEL, F. M. 1979. Tree regeneration strategies in lowland *Nothofagus*-dominated forest in south-central Chile. *Journal of Biogeography* 6:329-340.

WALKER, B. H. & NOY-MEIR, I. 1982. Aspects of stability and resilience of savanna ecosystems. Pp. 577-590 in Huntley, B. J. & Walker, N. H. (eds). *Ecological studies 42: ecology of tropical savannas* Springer-Verlag.

WALKER, J., MOORE, R. M. & ROBERTSON, J. A. 1972. Herbage response to tree and shrub thinning in *Eucalyptus populnea* shrub woodlands. *Australian Journal of Agricultural Research* 23:405-410.

WALTER, H. 1971. Natural savannas. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd.

WARCUP, J. H. 1980. Effect of heat treatment of forest soil on germination of buried seed. *Australian Journal of Botany* 28:567-571.

WEARING, C. H. & VAN EMDEN, H. F. 1967. Studies on the relations of insects and host plants. I. Effects of water stress in host plants on infestation by *Aphis fabae* Scop., *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). *Nature* 213:1051-1052.

WEBB, L. J., TRACEY, J. G. & HAYDOCK, K. P. 1967. A factor toxic to seedlings of the same species assoicated with living roots of the non-gregarious subtropical rainforest tree, *Grevillea robusta*. *Journal of Applied Ecology* 4:13-25.

WEBB, L. J., TRACEY, J. G. & WILLIAMS, W. T. 1972. Regeneration and pattern in the subtropical rainforest, *Journal of Ecology* 60:675-696.

WELLINGTON, A. B. 1984. Leaf water potentials, fire and the regeneration of mallee eucalypts in semi-arid, south-eastern Australia. *Oecologia* 64:360-362.

WELLINGTON, A. B. & NOBLE, I. R. 1985. Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology* 73:645-656.

WELLS, M. R. & VAN CUYLENBURG, H. R. M. 1978. *Land units of areas adjacent to the Tuyu and Yapilika forestry plantations, Melville Island, N.T. LC78/9* Land Conservation Unit, Territory Parks and Wildlife Commission, Darwin, N.T.

WELLS, M. R., VAN CUYLENBURG, H. R. M. & DUNLOP, C. R. 1978. *Land systems of the western half of Melville Island, N.T. LC78/10* Land Conservation Unit, Territory Parks and Wildlife Commission, Darwin, N.T.

WERNER, P. A. 1986. *Population dynamics and productivity of selected forest trees in Kakadu National Park.* Report to Australian National Parks and Wildlife Service.

WETTERHALL, R. L. 1975. *Bushfire disaster: an Australian community in crisis.* Angus and Robinson, Sydney.

WHITE, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50:905-909.

WHITMORE, T. C. 1975. *Tropical rainforests of the Far East.* Oxford University Press.

WHITMORE, T. C. 1982. On pattern and process in forests. Pp. 45-57 in Newman, E. J. (ed.). *The plant community as a working mechanism.* Blackwell, Oxford.

WILLARD, E. E. & MCKELL, C. M. 1973. Simulated grazing management systems in relation to shrub growth responses. *Journal of Range Management* 26:171-174.

WILLIAMS, J., PREBBLE, R. E., WILLIAMS, W. T. & HIGNETT, C. T. 1983. The influence of texture, structure and clay mineralogy on the soil moisture characteristic. *Australian Journal of Soil Research* 21:15-32.

WILLIAMS, J. E. 1990. The importance of herbivory in the population dynamics of three sub-alpine eucalypts in the Brindabella Range, south-east Australia. *Australian Journal of Ecology* 15:51-56.

WILLIAMSON, G. B. 1975. Pattern and seral composition in an old-growth beech-maple forest. *Ecology* 56:727-731.

WILSON, B. A. 1990. *The open forest-'treeless' plains boundary, Melville Island, Australia.* M. Sc. thesis. Department of Geography and Environmental Studies. University of Tasmania.

WILSON, B. A. & BOWMAN, D. M. J. S. 1987. Fire, storm, flood and drought: The vegetation ecology of Howard's Peninsula, Northern Territory. *Australian Journal of Ecology.* 12:165-174.

WILSON, B. A., BROCKLEHURST, P. S, CLARK, M. J. & DICKINSON, K. J. M 1990. *Vegetation survey of the Northern Territory, Australia: explanatory notes to accompany 1:1 000 000 vegetation map.* Technical Report 47. Conservation Commission of the Northern Territory.

WITHERS, J. & ASHTON, D. H. 1977. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. I The structure and regeneration. *Australian Journal of Botany* 25:623-637.

WOINARSKI, J. C. Z. & CULLEN, J. M. 1984. Distribution of invertebrates on foliage in forests of south-eastern Australia. *Australian Journal of Ecology* 9:207-232.

WOLDA, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* 47:369-381.

WOLDA, H. 1980. Seasonality of tropical insects: Leafhoppers (Homoptera) in Las Cumbres, Panama. *Journal of Animal Ecology* 49:277-290.

WOLDA, H. 1987. Seasonal cues in tropical organisms. Rainfall? Not necessarily! *Oecologia* 80:437-442.

WOODS, F. W., HARRIS, H. C. & CALDWELL, R. E. 1959. Monthly variations in carbohydrates and nitrogen in roots of sandhill oaks and wiregrass. *Ecology* 40:292-295.

YEN, A. L. 1989. Overstorey invertebrates in the Big Desert, Victoria. Pp. 285-299. in Noble, J. C. & Bradstock, R. A. (eds). *Mediterranean landscapes in Australia.* CSIRO.

Appendix 1 Correlation matrix of vegetation features and environmental variables for the entire Melville Island data set. The key to the abbreviations describing columns are provided with the row labels.

	Et	*Em*	*En*	*Ec*	Ds	Ba	1|2	2|2	1|3	2|3	3|3	T15	T45	T90	T150	G15	G45	G90	G150
Eucalyptus tetrodonta (Et)																			
Eucalyptus miniata (Em)	NS																		
Eucalyptus nesophila (En)	NS	NS																	
Erythrophleum chlorostachys (Ec)	NS	NS	NS																
Deciduous tree species (Ds)	NS	-1	-1	2															
Basal area (Ba)	NS	NS	NS	NS	NS														
Kyst 1/2	4	3	NS	NS	NS	NS													
Kyst 2/2	NS	NS	NS	-3	-3	-3	NS												
Kyst 1/3	4	4	NS	NS	NS	NS	4	NS											
Kyst 2/3	NS	NS	NS	-3	-3	-4	NS	4	NS										
Kyst 3/3	NS	3	NS	NS	NS	NS	NS	NS	NS	NS									
Texture-15 cm (T15)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-4								
Texture-45 cm (T45)	NS	2	NS	NS	NS	NS	-4	NS	-2	NS	-4	3							
Texture-90 cm (T90)	-2	1	NS	NS	NS	NS	-4	-1	-4	-4	-4	1	NS						
Texture-150 cm (T150)	-1	NS	NS	NS	NS	NS	-3	-3	-4	-4	-1	NS	4	4					
% gravel-15 cm(G15)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	NS	4	NS	NS				
% gravel-45 cm (G45)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	3	4	NS	4			
% gravel-90 cm (G90)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	4	NS	1	4		
% gravel-150 cm (G150)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	1	NS	4	
% water-15 cm (November)	NS	NS	NS	NS	NS	NS	-1	NS	-1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-45 cm (November)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	3	3	NS	NS	NS	NS	NS	NS
% water-90 cm (November)	NS	NS	NS	NS	NS	NS	-1	NS	-3	NS	NS	3	3	4	3	NS	3	NS	NS
% water-150 cm (November)	NS	NS	NS	NS	NS	NS	-3	NS	-4	NS	NS	3	4	4	4	3	3	NS	NS
% water-15 cm (February)	NS	NS	NS	NS	NS	NS	-3	-2	-3	-1	NS	NS	NS	1	1	3	NS	NS	NS
% water-45 cm (February)	NS	NS	NS	NS	NS	NS	-3	NS	-3	NS	NS	1	1	3	1	NS	NS	NS	NS
% water-90 cm (February)	NS	NS	NS	NS	NS	NS	-2	-1	-3	-1	NS	3	3	4	3	NS	NS	NS	NS
% water-150 cm (February)	-1	NS	NS	NS	NS	NS	-1	-1	-1	-1	-2	3	4	4	4	NS	NS	NS	NS
% water-15 cm (April)	NS	NS	NS	NS	NS	NS	-1	-1	-1	-1	NS	1	NS	1	2	NS	NS	NS	NS
% water-45 cm (April)	NS	NS	NS	NS	NS	NS	-3	NS	-3	NS	NS	2	2	3	3	NS	NS	NS	NS
% water-90 cm (April)	NS	NS	NS	NS	NS	NS	-3	NS	-3	NS	-1	3	4	4	4	1	3	NS	NS
% water-150 cm (April)	NS	NS	NS	NS	NS	NS	-3	-1	-4	-2	-3	2	4	4	4	2	4	4	NS
% water-15 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	NS	NS	NS
% water-45 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	2	3	NS	NS	NS	NS	NS	NS
% water-90 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	3	4	4	3	NS	NS	NS	NS
% water-150 cm (June)	NS	NS	NS	NS	NS	NS	NS	-3	NS	-4	-4	NS	2	4	4	NS	NS	NS	NS
% water-15 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	3	NS	NS	NS	NS	NS	NS	NS
% water-45 cm (September)	NS	NS	NS	NS	NS	NS	NS	1	NS	NS	NS	4	4	NS	NS	NS	NS	NS	NS
% water-90 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	4	4	4	4	NS	NS	NS	NS
% water-150 cm (September)	NS	NS	NS	NS	NS	2	NS	NS	NS	-3	-3	1	4	4	4	NS	NS	NS	NS
Water potential-15 cm (November)	NS	1	NS	NS	NS	3	4	NS	3	NS	NS	NS	-3	-3	-1	-3	-4	NS	NS
Water potential-45 cm (November)	NS	NS	NS	NS	NS	NS	4	3	NS	2	NS	NS	NS	NS	-1	NS	-3	NS	NS
Water potential-90 cm (November)	NS	NS	NS	NS	NS	NS	NS	3	4	2	NS	NS	NS	NS	-1	NS	-3	NS	NS
Water potential-150 cm (November)	NS	NS	NS	NS	NS	NS	3	NS	3	NS	NS	-3	-2	-1	NS	NS	NS	NS	-4
Water potential-15 cm (February)	NS	1	NS	2	NS	NS	4	NS	4	NS	2	NS	-1	-4	-4	-1	-4	NS	NS
Water potential-45 cm (February)	1	NS	NS	NS	NS	NS	NS	3	4	3	NS	-3	-1	-4	-3	NS	-3	-1	NS
Water potential-90 cm (February)	1	NS	NS	NS	NS	NS	4	3	NS	3	NS	-3	-1	-4	-3	NS	NS	-1	NS
Water potential-150 cm (February)	NS	NS	NS	NS	NS	-1	3	2	3	2	NS	NS	NS	-3	-1	NS	NS	NS	NS
Water potential-15 cm (April)	NS	NS	NS	NS	NS	NS	1	NS	2	NS	NS	NS	NS	-4	-4	-1	-4	-3	NS
Water potential-45 cm (April)	NS	NS	NS	NS	NS	NS	NS	3	NS	3	NS	NS	NS	NS	-3	NS	-4	-3	NS
Water potential-90 cm (April)	NS	NS	NS	NS	NS	NS	NS	3	NS	3	NS	NS	NS	NS	-3	NS	NS	-3	NS
Water potential-150 cm (April)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	-4
Water potential-15 cm (June)	NS	NS	NS	NS	NS	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	NS	NS
Water potential-45 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1	NS	NS	NS	NS	NS	-3
Water potential-90 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS		NS	NS	NS	NS	NS	NS
Water potential-150 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	1	NS	-3	-1	NS	NS	NS	NS	NS	-3
Water potential-15 cm (September)	NS	NS	NS	NS	NS	-1	NS	NS	NS	NS	NS	-2	-3	NS	NS	-3	NS	NS	NS
Water potential-45 cm (September)	NS	NS	NS	NS	NS	-1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-90 cm (September)	NS	NS	NS	NS	NS	-2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-150 cm (September)	NS	NS	NS	NS	NS	-2	NS	NS	NS	NS	NS	-4	-3	-1	NS	NS	NS	NS	-4

1- P<0.01, 2- P<0.02, 3- P<0.01, 4- P<0.001
Negative correlations are indicated

Appendix 1 continued

	Et	*Em*	*Er*	*Ec*	Ds	Ba	112	212	113	213	313	T15	T45	T90	T150	G15	G45	G90	G150
Conductivity	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	1	NS	1	2	NS	1	1	NS
pH	NS	3	NS	4	NS	NS	4	NS	4	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Available N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Available P	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Available K	NS	NS	NS	NS	NS	4	1	-1	1	-3	NS	NS	NS	NS	NS	NS	NS	NS	NS
Available Ca	NS	NS	NS	3	NS	1	2	-3	2	-4	NS	1	NS	NS	NS	NS	NS	NS	NS
Available Mg	NS	NS	NS	4	NS	NS	3	-2	3	-2	NS	NS	NS	NS	NS	NS	NS	NS	NS

1- P<0.01, 2- P<0.02, 3- P<0.01, 4- P<0.001
Negative correlations are indicated

Appendix 2 Correlation matrix of vegetation features and environmental variables for the forest plots only. The key to the abbreviations describing columns are provided with the row labels.

	Et	*Em*	*En*	*Ec*	Ds	Ba	112	212	113	213	313
Eucalyptus tetrodonta (Et)											
Eucalyptus miniata (Em)	NS										
Eucalyptus nesophila (En)	NS	NS									
Erythrophleum chlorostachys (Ec)	-4	NS	NS								
Deciduous tree species (Ds)	NS	-1	NS	3							
Basal area (Ba)	NS	NS	NS	NS	NS						
Kyst 1/2	-1	NS	NS	NS	NS	NS					
Kyst 2/2	NS	NS	NS	-4	NS	-3	NS				
Kyst 1/3	-2	NS	NS	NS	NS	NS	4	NS			
Kyst 2/3	NS	3	NS	NS	NS	NS	NS	-4	NS		
Kyst 3/3	NS	NS	NS	-4	NS	-3	NS	NS	NS	NS	
Texture-15 cm (T15)	NS	NS	NS	NS	NS	NS	-2	NS	-3	NS	NS
Texture-45 cm (T45)	NS	-1	NS	NS	NS	NS	NS	NS	NS	NS	-2
Texture-90 cm (T90)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-3
Texture-150 cm (T150)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-2
% gravel-15 cm(G15)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% gravel-45 cm (G45)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% gravel-90 cm (G90)	NS	NS	NS	NS	NS	NS	NS	NS	NS	-3	-3
% gravel-150 cm (G150)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-15 cm (November)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-1
% water-45 cm (November)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-2
% water-90 cm (November)	NS	NS	NS	NS	NS	NS	NS	-3	NS	1	1
% water-150 cm (November)	NS	NS	1	NS	NS	NS	NS	-1	NS	NS	NS
% water-15 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-45 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-90 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-150 cm (February)	NS	NS	NS	NS	NS	1	NS	NS	NS	NS	NS
% water-15 cm (April)	NS	NS	NS	NS	NS	NS	-1	NS	-2	NS	NS
% water-45 cm (April)	NS	NS	NS	NS	NS	NS	-3	NS	-2	NS	NS
% water-90 cm (April)	NS	NS	NS	NS	NS	NS	NS	-1	NS	NS	NS
% water-150 cm (April)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-15 cm (June)	1	NS	-1	NS	NS	NS	NS	NS	-1	NS	NS
% water-45 cm (June)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-90 cm (June)	NS	NS	NS	NS	NS	NS	-1	NS	-1	NS	NS
% water-150 cm (June)	NS	NS	NS	NS	NS	NS	-3	NS	-3	NS	NS
% water-15 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-45 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-90 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% water-150 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-15 cm (November)	NS	1	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-45 cm (November)	NS	NS	NS	NS	NS	NS	-2	1	NS	-1	-2
Water potential-90 cm (November)	NS	NS	NS	NS	NS	NS	-2	1	NS	-1	-2
Water potential-150 cm (November)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-15 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-45 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-90 cm (February)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-150 cm (February)	NS	NS	NS	NS	NS	-3	NS	NS	NS	NS	NS
Water potential-15 cm (April)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-45 cm (April)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-90 cm (April)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-150 cm (April)	NS	NS	1	NS	NS	NS	1	NS	3	NS	NS
Water potential-15 cm (June)	NS	NS	NS	NS	NS	1	NS	NS	NS	NS	NS
Water potential-45 cm (June)	NS	NS	1	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-90 cm (June)	NS	NS	1	NS	NS	NS	NS	NS	NS	NS	NS
Water potential-150 cm (June)	NS	NS	NS	NS	NS	-1	NS	NS	NS	NS	NS
Water potential-15 cm (September)	NS	NS	NS	NS	NS	-1	NS	NS	NS	NS	NS
Water potential-45 cm (September)	NS	1	NS	NS	NS	-2	NS	NS	NS	NS	NS
Water potential-90 cm (September)	NS	1	NS	NS	NS	-2	NS	NS	NS	NS	NS
Water potential-150 cm (September)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

1- P<0.01, 2- P<0.02, 3- P<0.01, 4- P<0.001
Negative correlations are indicated

Appendix 2 continued

	Et	*Em*	*En*	*Ec*	Ds	Ba	112	212	113	213	313
Conductivity	NS	NS	NS	NS	NS	NS	NS	-3	NS	NS	-4
pH	NS	3	NS	NS	NS	NS	NS	-3	-3	3	NS
Available N	NS	NS	NS	NS	NS	NS	NS	NS	NS	3	NS
Available P	NS	NS	NS	NS	NS	NS	1	NS	1	NS	NS
Available K	NS	NS	NS	NS	4	NS	NS	NS	NS	NS	NS
Available Ca	NS	NS	NS	NS	NS	NS	-4	NS	2	-4	NS
Available Mg	NS	NS	NS	1	NS	NS	-4	NS	1	-3	NS

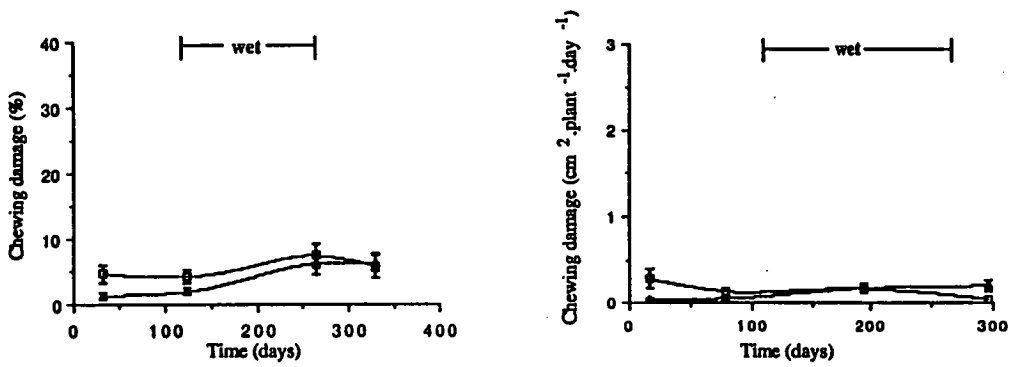
1- P<0.01, 2- P<0.02, 3- P<0.01, 4- P<0.001
Negative correlations are indicated

Appendix 3 Soil chemical attributes for the sites numbered on Figs. 6-11.

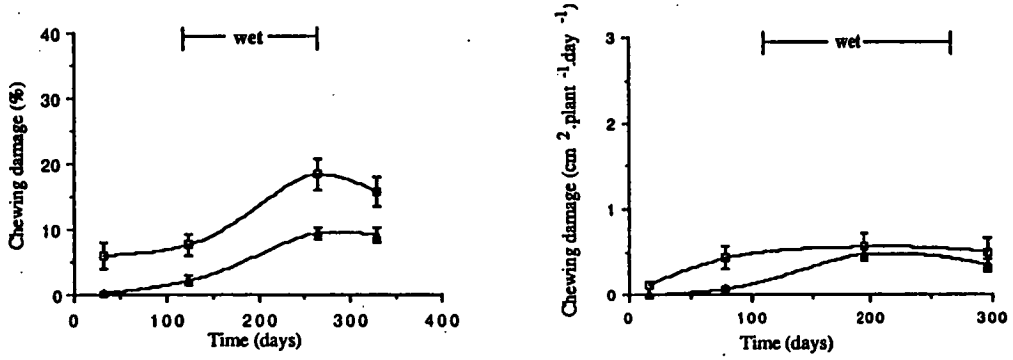
Site no.	Conductivity	pH	Available N	Available P	Available K	Available Ca	Available Mg
1	0.08	5.05	42	<5	36	198	176
2	0.04	5.2	84	<5	20	62	25
3	0.06	5	56	<5	31	119	61
4	0.1	4.6	70	<5	34	36	16
5	0.1	4.75	112	<5	42	59	29
6	0.1	4.5	126	<5	35	40	34
7	0.12	4.6	56	13	39	117	125
8	0.04	5	56	<5	32	45	47
9	0.13	5.15	56	5	44	565	147
10	0.14	5.3	63	6	47	703	245
11	0.07	4.6	42	5	23	67	40
12	0.1	5	70	<5	51	179	140
13	0.08	5.3	56	9	43	318	105
14	0.06	5	84	18	26	71	51
15	0.05	4.8	56	<5	26	41	13
16	0.05	5.4	49	<5	36	268	66
17	0.06	5.3	49	<5	47	182	84
18	0.07	5.1	56	<5	50	103	55
19	0.14	4.85	84	9	121	122	171
20	0.1	5.8	42	<5	137	730	149
21	0.09	5.2	63	<5	55	233	102
22	0.08	5.8	112	<5	43	259	140
23	0.08	5.75	70	<5	49	500	213
24	0.06	4.75	70	<5	34	71	48
25	0.06	4.8	42	<5	32	82	48
26	0.11	5.1	63	<5	76	202	118

Appendix 4 Mean (and s.e.m.) insect damage, in terms of the damage condition of the plant and rate of leaf consumption for eight tree species in two vegetation types (▲ forest, □ low forest). The wet season period is indicated. **a)** Chewing damage.

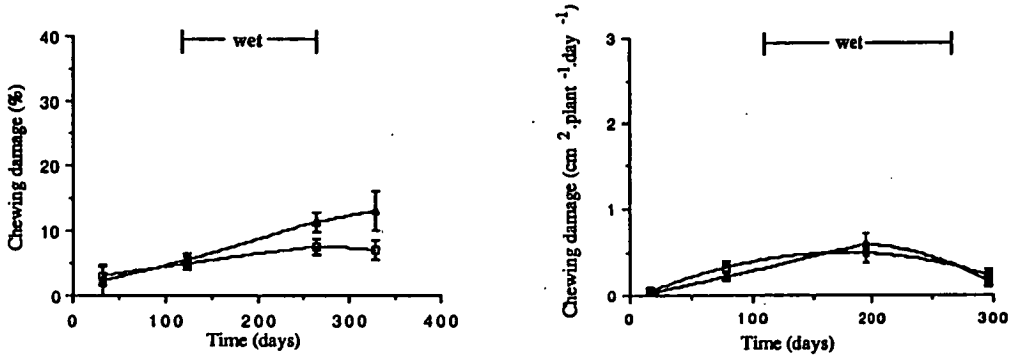
Buchanania obovata



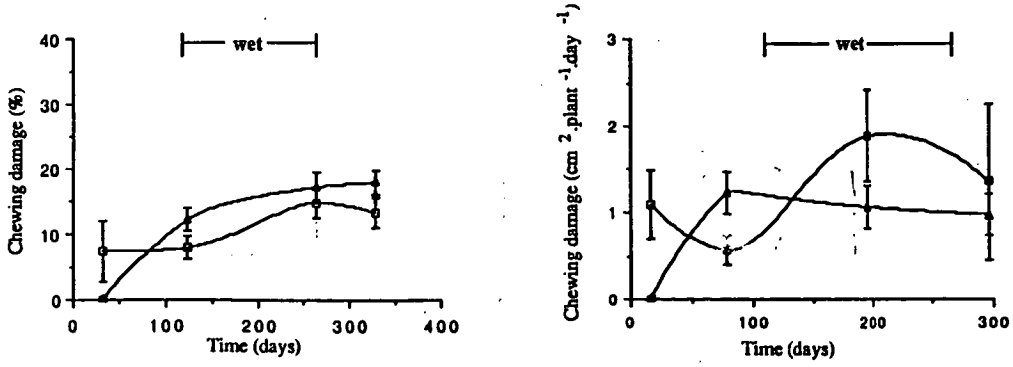
Planchonia careya



Terminalia ferdinandiana

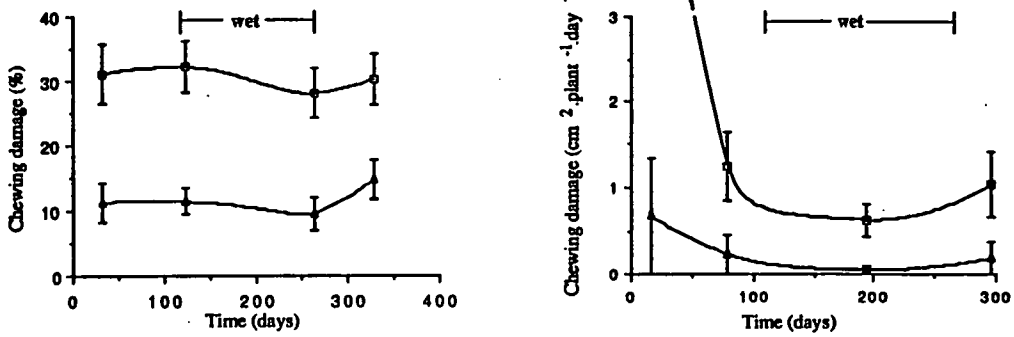


Erythrophleum chlorostachys

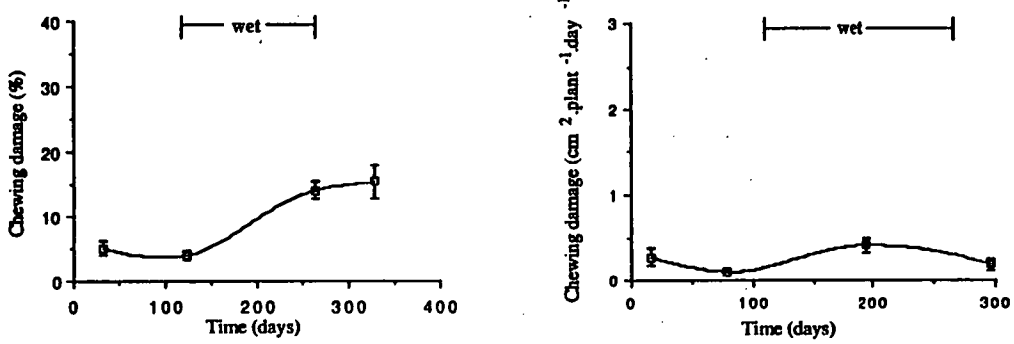


Appendix 4 a) continued

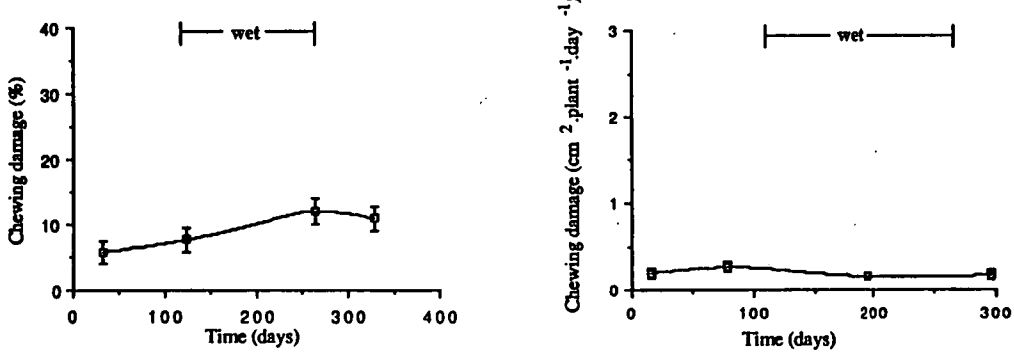
Eucalyptus confertiflora



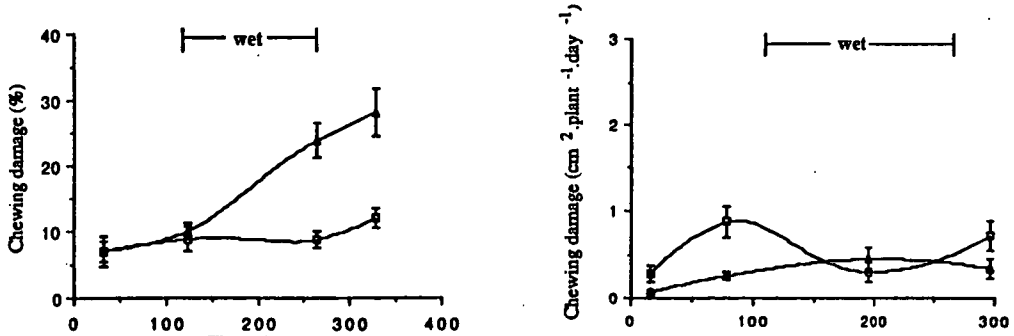
Eucalyptus miniata



Eucalyptus tetrodonta

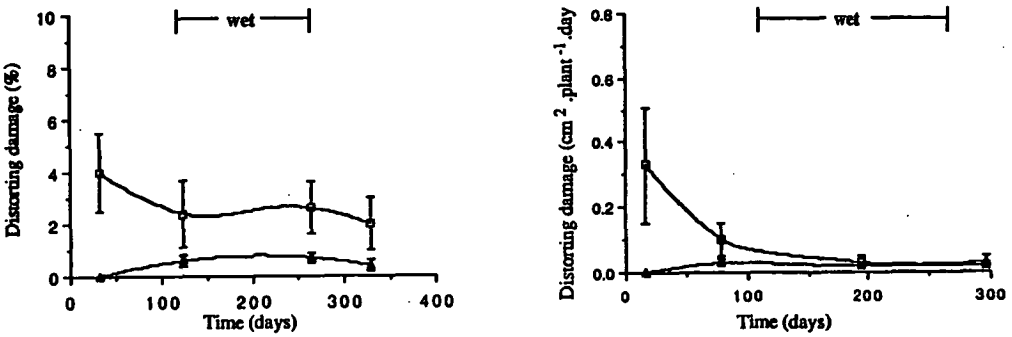


Acacia aulacocarpa

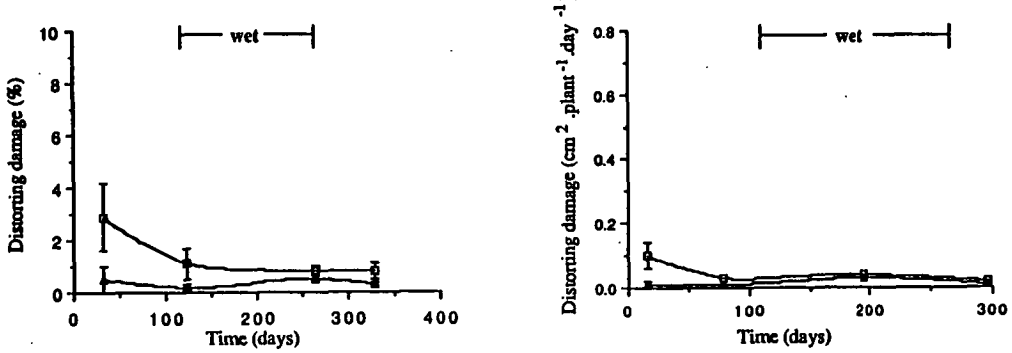


Appendix 4 b) distorting damage.

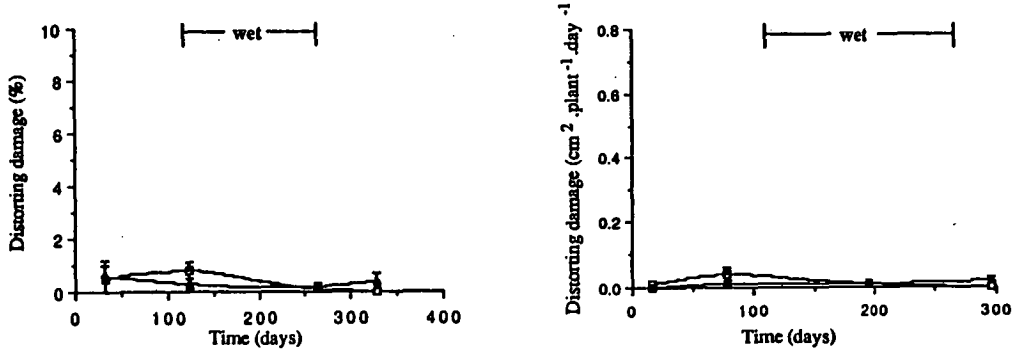
Buchanania obovata



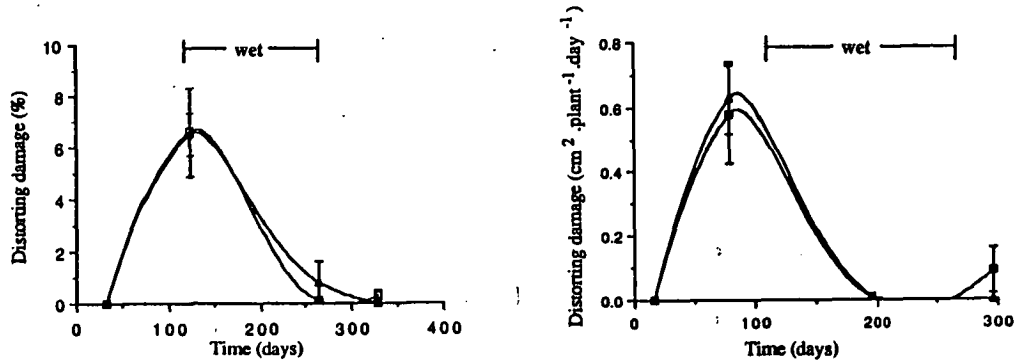
Planchonia careya



Terminalia ferdinandiana

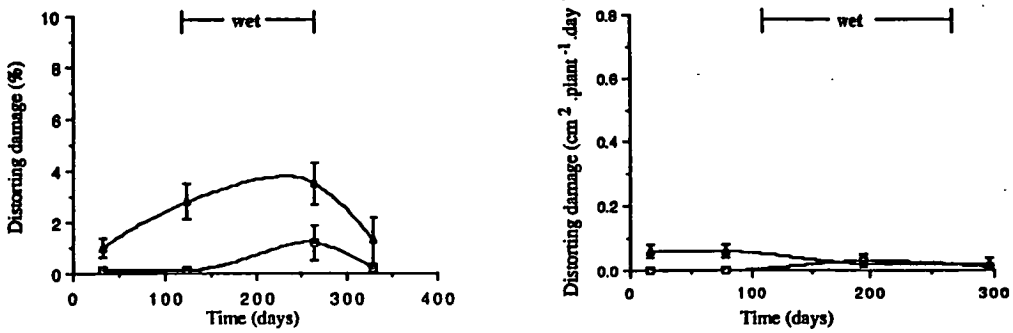


Erythrophleum chlorostachys

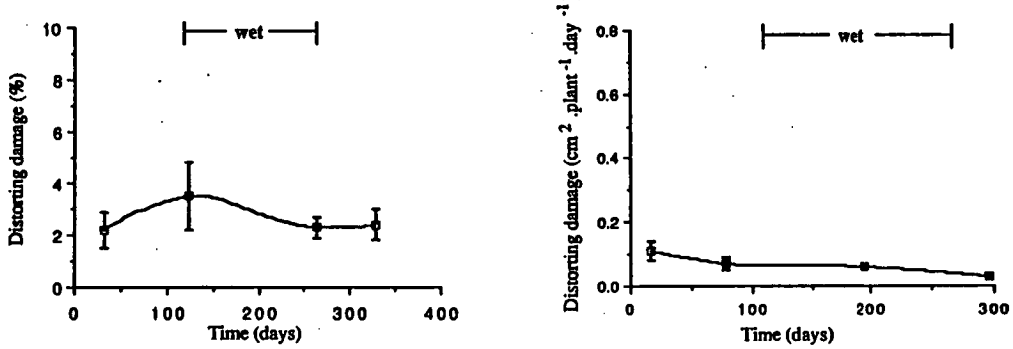


Appendix 4b) continued

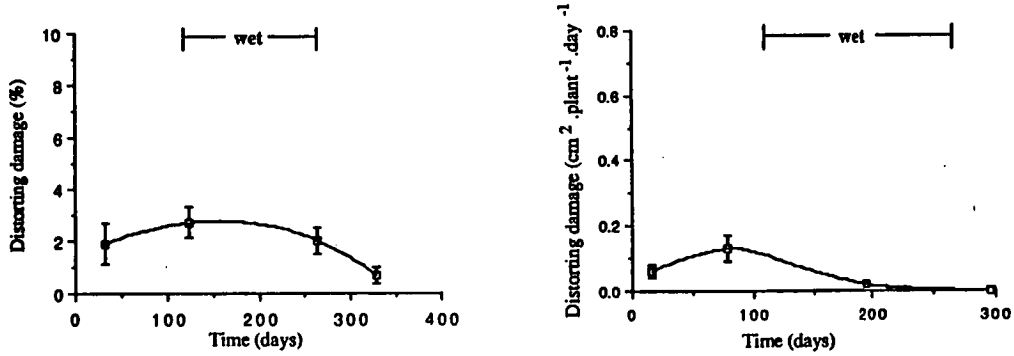
Eucalyptus confertiflora



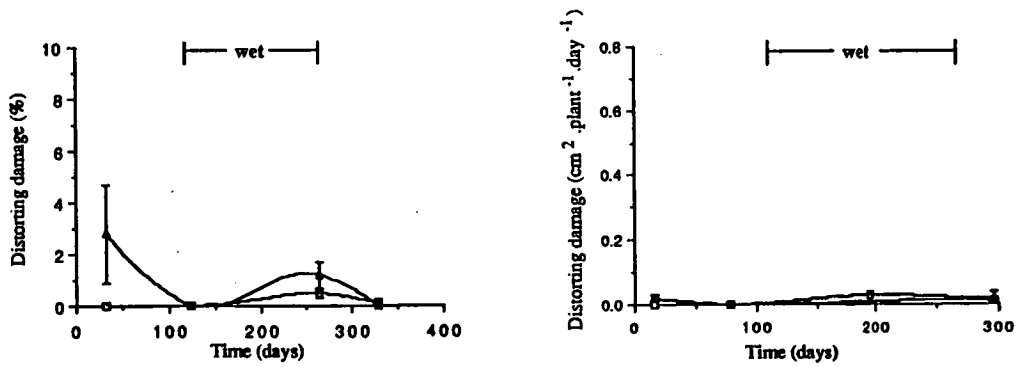
Eucalyptus miniata



Eucalyptus tetrodonta

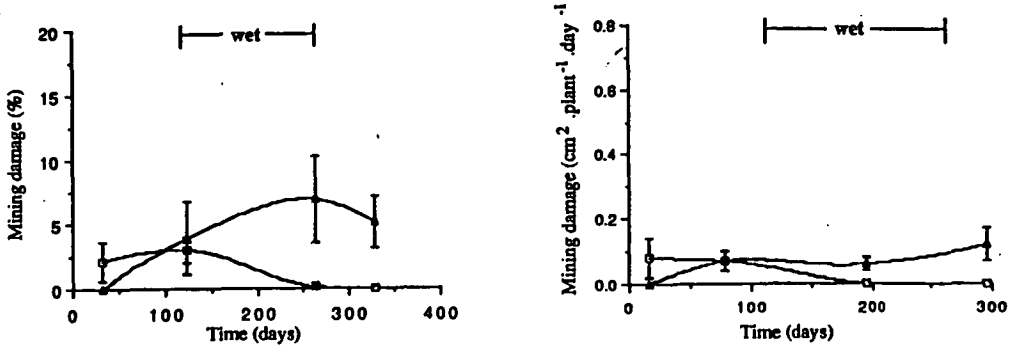


Acacia aulacocarpa

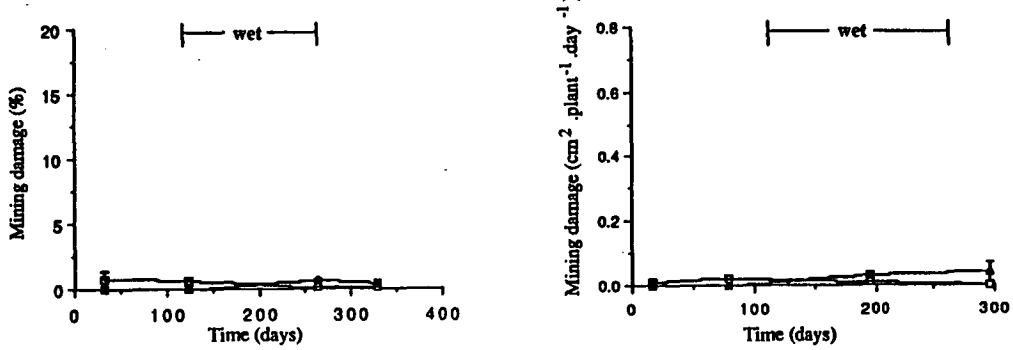


Appendix 4 c) mining damage.

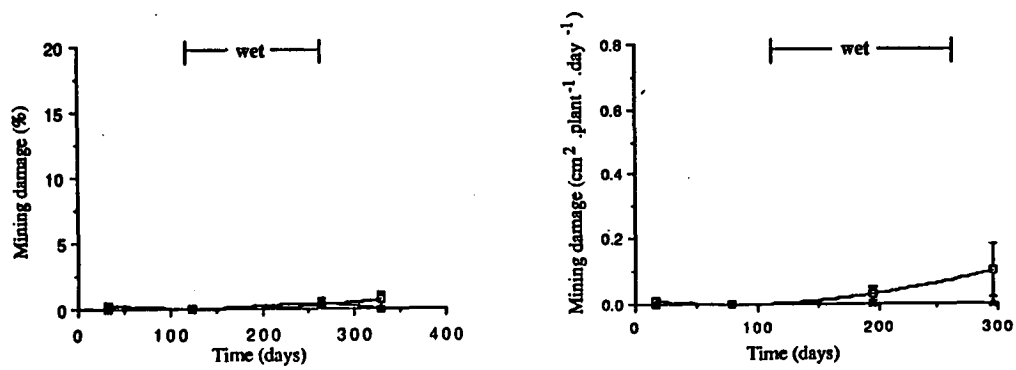
Buchanania obovata



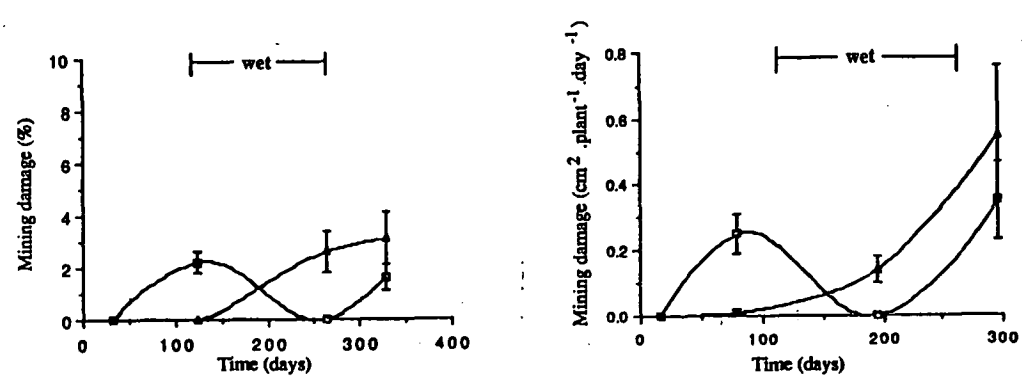
Planchonia careya



Terminalia ferdinandiana

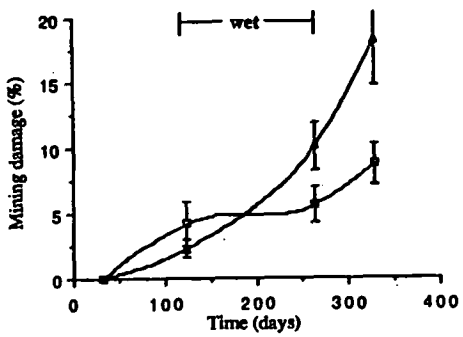


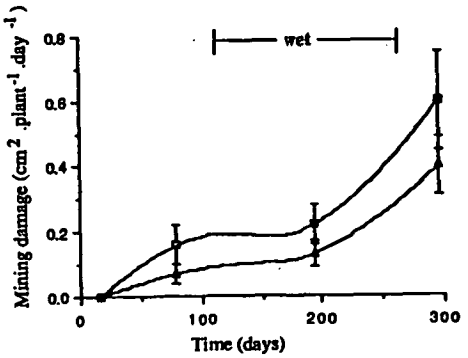
Erythrophleum chlorostachys



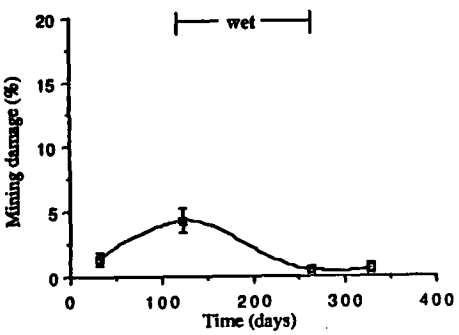
Appendix 4 c) continued

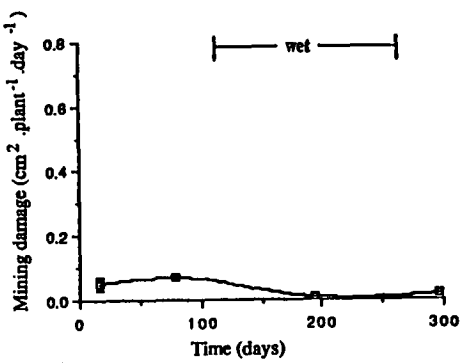
Eucalyptus confertiflora



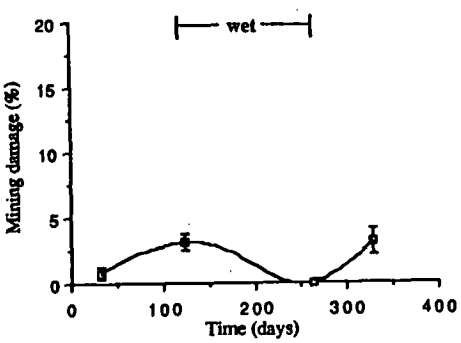


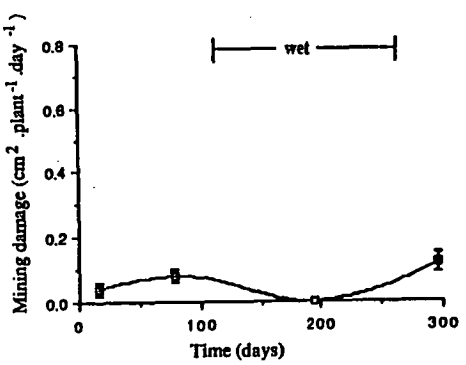
Eucalyptus miniata



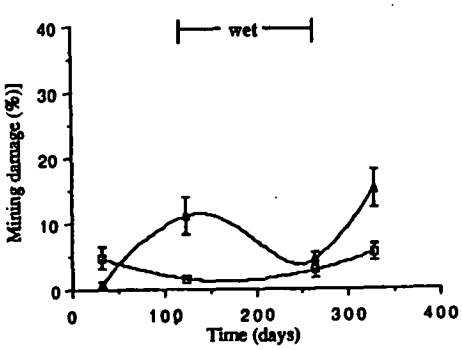


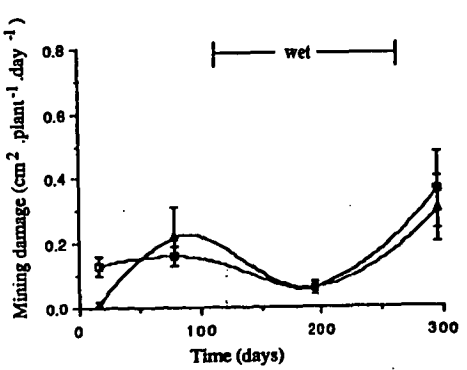
Eucalyptus tetrodonta





Acacia aulacocarpa





Appendix 5 Distribution of insect taxa according to sample: BO *Buchanania obovata*; PC *Planchonia careya*; EC *Erythrophleum chlorostachys*; CO *Eucalyptus confertiflora*; EM *Eucalyptus miniata*; ET *Eucalyptus tetrodonta*; AA *Acacia aualacocarpa*; TF *Terminalia ferdinandiana*; F forest; LF low forest; M Milikapiti.

Sample	Plant biomass	Psylloidea	Cixiidae	Fulgoridae	Dictyopharidae	Tropiduchidae
BO F Aug	478.32	0	0	2	3	1
PC F Aug	366.61	0	0	4	0	2
EC F Aug	642.75	139	0	10	2	1
CO F Aug	369.56	0	0	1	2	0
EM F Aug	750.68	63	0	11	3	0
ET F Aug	784.01	7	0	0	0	3
AA F Aug	215.32	9	0	0	0	0
BO LF Aug	435.82	11	3	17	3	0
PC LF Aug	392.6	3	0	13	0	2
EC LF Aug	546.7	944	0	12	2	0
CO LF Aug	410.99	0	0	8	1	0
AA LF Aug	148.51	10	0	0	2	0
BO F Jan	517.52	0	0	0	2	0
PC F Jan	900.44	0	0	0	0	0
TF F Jan	864.6	0	0	0	1	1
EC F Jan	1565.6	0	0	0	0	0
CO F Jan	590.26	0	0	0	1	1
EM F Jan	1665.02	0	0	0	2	2
ET F Jan	987.31	0	0	0	0	0
AA F Jan	530.83	0	0	0	0	0
BO LF Jan	587.39	0	0	0	0	0
PC LF Jan	1027.49	0	0	0	3	2
TF LF Jan	433.32	0	0	1	2	11
EC LF Jan	680.24	0	0	1	2	0
CO LF Jan	503.05	0	0	3	0	1
AA LF Jan	448.44	0	0	0	0	0
BO F Jan SB	321.47	0	0	1	0	0
PC F Jan SB	958.66	0	0	1	0	0
TF F Jan SB	881.35	0	0	1	5	0
EC F Jan SB	808.29	1	0	0	0	1
CO F Jan SB	1040.65	0	0	0	1	0
EM F Jan SB	1921.95	0	0	1	0	0
ET F Jan SB	1081.59	44	0	0	0	0
AA F Jan SB	574.85	0	0	0	0	0
BO F May	541.94	0	0	4	0	1
PC F May	1191.95	0	0	12	3	6
TF F May	866.91	0	0	0	4	5
EC F May	963.62	0	0	5	0	0
CO F May	541	0	0	0	0	0
EM F May	2173.78	0	0	4	0	2
ET F May	970.37	0	0	4	0	0
AA F May	498.59	0	0	1	1	1
BO LF May	1013.55	0	0	2	0	0
PC LF May	1316.17	0	0	13	1	18
TF LF May	891.15	0	0	0	1	1
EC LF May	1015	2	0	1	0	0
CO LF May	590.07	0	0	4	0	0
AA LF May	474.14	1	0	1	0	2

Appendix 5 continued

Sample	Delphacidae	Cicadellidae	Flatidae	Eurybrachyidae	Membracidae	Achilidae	Derbidae
BO F Aug	4	2	1	0	0	0	0
PC F Aug	2	5	1	0	0	0	0
EC F Aug	4	1	3	0	0	0	0
CO F Aug	3	20	3	0	0	0	0
EM F Aug	10	32	34	0	0	0	0
ET F Aug	5	28	5	0	0	0	0
AA F Aug	1	0	0	0	0	0	0
BO LF Aug	3	7	0	0	0	0	0
PC LF Aug	1	2	1	0	0	0	0
EC LF Aug	8	0	0	0	0	0	0
CO LF Aug	2	23	1	0	0	0	0
AA LF Aug	1	2	1	0	1	0	0
BO F Jan	0	8	0	0	0	1	0
PC F Jan	0	1	0	0	0	0	0
TF F Jan	3	20	0	1	0	1	0
EC F Jan	2	0	1	0	0	0	0
CO F Jan	2	6	1	1	0	0	0
EM F Jan	4	19	8	0	0	1	1
ET F Jan	0	3	0	0	0	0	0
AA F Jan	0	1	1	0	0	0	0
BO LF Jan	1	14	0	0	0	0	0
PC LF Jan	0	0	0	1	0	1	0
TF LF Jan	2	1	1	0	0	3	0
EC LF Jan	3	1	0	0	0	0	0
CO LF Jan	2	7	2	32	0	0	0
AA LF Jan	0	0	0	0	34	0	0
BO F Jan M	0	2	0	0	0	0	0
PC F Jan M	0	0	0	0	0	0	0
TF F Jan M	0	2	1	1	0	0	0
EC F Jan M	0	2	1	0	0	0	0
CO F Jan M	3	1	0	0	0	0	0
EM F Jan M	0	7	2	0	1	0	0
ET F Jan M	3	0	1	0	0	0	0
AA F Jan M	0	5	0	0	0	0	0
BO F May	2	3	2	0	0	0	0
PC F May	4	4	7	1	0	0	0
TF F May	4	2	4	1	0	0	0
EC F May	0	2	1	0	0	0	0
CO F May	0	5	2	0	0	0	0
EM F May	3	8	11	0	0	0	0
ET F May	1	4	1	1	1	0	0
AA F May	1	1	2	0	0	0	0
BO LF May	1	146	0	0	0	0	0
PC LF May	1	2	13	0	0	0	2
TF LF May	1	0	1	0	0	0	0
EC LF May	0	1	1	1	0	0	0
CO LF May	0	4	4	1	0	0	0
AA LF May	1	0	1	0	0	0	0

Appendix 5 continued

Sample	Ricaniidae	Pseudococcidea	unidentified Homoptera	Alydidae	Tingidae	Pentatomidae	Miridae
BO F Aug	4	0	1	0	0	0	0
PC F Aug	6	0	1	0	0	0	0
EC F Aug	1	0	1	0	0	0	0
CO F Aug	0	0	3	0	0	0	0
EM F Aug	2	18	2	0	0	0	0
ET F Aug	0	8	6	0	0	0	0
AA F Aug	0	0	1	0	0	0	0
BO LF Aug	1	0	0	0	0	0	0
PC LF Aug	0	0	0	0	0	0	0
EC LF Aug	1	0	0	0	0	0	0
CO LF Aug	0	0	1	0	0	0	0
AA LF Aug	0	0	1	0	0	0	0
BO F Jan	0	0	1	0	0	0	0
PC F Jan	0	0	0	0	0	0	1
TF F Jan	0	0	0	0	0	0	0
EC F Jan	0	0	0	0	0	0	0
CO F Jan	0	10	1	0	0	0	0
EM F Jan	0	4	8	0	0	0	0
ET F Jan	0	6	0	0	0	0	0
AA F Jan	0	0	0	0	0	0	0
BO LF Jan	0	0	1	0	0	0	0
PC LF Jan	0	0	0	0	0	0	0
TF LF Jan	2	0	2	0	0	0	0
EC LF Jan	0	0	0	0	0	0	0
CO LF Jan	0	1	0	0	0	0	0
AA LF Jan	0	0	2	1	0	0	0
BO F Jan M	0	0	0	0	1	1	0
PC F Jan M	0	0	2	0	0	0	0
TF F Jan M	0	0	0	0	0	0	0
EC F Jan M	0	0	2	0	0	1	1
CO F Jan M	0	0	1	0	0	0	0
EM F Jan M	0	41	0	0	0	1	0
ET F Jan M	0	2	0	0	0	0	0
AA F Jan M	0	0	0	0	0	0	0
BO F May	2	0	4	1	0	0	0
PC F May	11	0	1	0	0	0	0
TF F May	10	0	0	1	0	0	0
EC F May	2	2	1	0	0	0	0
CO F May	1	0	0	0	0	0	0
EM F May	0	4	1	0	0	0	0
ET F May	0	1	4	0	0	0	0
AA F May	0	14	1	1	0	1	0
BO LF May	1	0	4	0	0	0	0
PC LF May	19	0	1	0	0	0	0
TF LF May	1	0	0	0	0	0	0
EC LF May	1	0	1	0	0	0	0
CO LF May	5	0	1	0	0	0	0
AA LF May	0	131	0	0	0	0	0

Appendix 5 continued

Sample	Coreidae	unidentified Heteroptera	Eumastacidae	Gryllidae	Acrididae	Tettigoniidae
BO F Aug	0	0	0	3	0	1
PC F Aug	0	0	0	4	1	0
EC F Aug	0	0	1	4	0	0
CO F Aug	0	0	0	3	0	2
EM F Aug	0	0	0	1	0	2
ET F Aug	0	0	0	4	0	0
AA F Aug	0	0	0	0	0	0
BO LF Aug	0	0	0	2	0	0
PC LF Aug	0	0	0	0	0	0
EC LF Aug	0	0	9	1	0	0
CO LF Aug	0	0	1	4	2	0
AA LF Aug	0	0	0	0	0	0
BO F Jan	0	0	1	7	1	3
PC F Jan	0	0	1	4	1	3
TF F Jan	0	0	0	3	0	1
EC F Jan	0	0	5	2	0	3
CO F Jan	0	0	1	3	3	2
EM F Jan	0	0	4	2	2	0
ET F Jan	0	0	1	2	1	2
AA F Jan	0	0	1	4	0	1
BO LF Jan	0	0	0	1	2	1
PC LF Jan	0	0	0	0	1	10
TF LF Jan	0	0	0	1	0	9
EC LF Jan	0	0	1	0	1	6
CO LF Jan	0	0	0	2	5	7
AA LF Jan	0	0	2	4	0	0
BO F Jan M	0	0	0	1	1	1
PC F Jan M	0	0	0	1	1	3
TF F Jan M	0	0	1	1	1	4
EC F Jan M	0	0	4	2	0	0
CO F Jan M	0	0	0	1	0	3
EM F Jan M	1	0	0	0	1	0
ET F Jan M	0	0	0	0	1	1
AA F Jan M	0	0	0	0	0	0
BO F May	0	1	2	3	0	0
PC F May	0	0	1	5	0	2
TF F May	0	0	3	2	0	0
EC F May	0	0	8	0	0	0
CO F May	0	0	6	2	0	0
EM F May	0	0	4	4	0	0
ET F May	0	0	2	1	0	1
AA F May	0	0	4	3	0	3
BO LF May	0	0	2	0	1	0
PC LF May	0	0	0	3	0	2
TF LF May	0	1	1	1	0	1
EC LF May	0	0	7	2	0	1
CO LF May	0	0	0	3	2	1
AA LF May	0	0	5	2	1	1

Appendix 5 continued

Sample	Stenopelmatidae	unidentified Orthoptera	Hispinae	Erirrhininae	Bruchidae	Chrysomelinae
BO F Aug	0	0	0	0	0	0
PC F Aug	0	0	0	0	0	0
EC F Aug	0	0	0	0	0	0
CO F Aug	0	0	0	0	0	0
EM F Aug	0	0	0	0	0	0
ET F Aug	0	0	0	0	0	0
AA F Aug	0	0	0	0	0	0
BO LF Aug	0	0	0	0	0	13
PC LF Aug	0	1	0	0	0	0
EC LF Aug	0	1	0	0	0	0
CO LF Aug	0	1	0	0	0	0
AA LF Aug	0	1	0	0	0	0
BO F Jan	0	1	0	0	0	0
PC F Jan	0	1	0	0	0	4
TF F Jan	0	2	0	0	1	0
EC F Jan	0	1	0	0	0	0
CO F Jan	0	6	0	0	0	0
EM F Jan	0	1	0	0	0	0
ET F Jan	0	0	0	0	0	0
AA F Jan	0	0	0	0	0	1
BO LF Jan	0	0	0	0	0	0
PC LF Jan	0	1	0	0	1	0
TF LF Jan	0	2	0	0	0	2
EC LF Jan	0	1	0	0	0	1
CO LF Jan	1	1	0	0	0	2
AA LF Jan	0	1	0	0	0	3
BO F Jan M	1	0	0	0	0	1
PC F Jan M	0	0	0	0	0	2
TF F Jan M	0	1	0	0	0	2
EC F Jan M	0	0	0	0	0	2
CO F Jan M	0	0	0	0	0	1
EM F Jan M	0	1	0	0	0	1
ET F Jan M	0	0	0	0	0	0
AA F Jan M	0	0	0	0	0	2
BO F May	1	0	0	0	0	1
PC F May	0	2	0	0	1	5
TF F May	0	2	0	0	0	0
EC F May	1	4	0	1	0	1
CO F May	0	0	0	0	0	0
EM F May	0	0	0	0	0	1
ET F May	0	0	0	0	0	0
AA F May	0	0	0	0	0	2
BO LF May	2	1	0	0	0	0
PC LF May	5	1	0	0	0	0
TF LF May	0	0	0	0	0	1
EC LF May	0	1	0	0	0	0
CO LF May	1	1	0	0	0	1
AA LF May	0	3	1	0	0	1

Appendix 5 continued

Sample	Cryptocephalinae	Alleculidae	Scolytinae	Otiorrhynchinae	Cryptorrhynchinae
BO F Aug	0	0	0	0	0
PC F Aug	0	0	0	0	0
EC F Aug	0	0	0	0	0
CO F Aug	0	0	0	4	0
EM F Aug	0	0	0	4	0
ET F Aug	0	0	0	4	0
AA F Aug	0	0	0	1	0
BO LF Aug	1	0	0	0	1
PC LF Aug	0	0	0	0	0
EC LF Aug	0	0	2	0	0
CO LF Aug	0	0	0	0	0
AA LF Aug	0	0	0	0	0
BO F Jan	0	0	0	4	0
PC F Jan	0	0	0	3	0
TF F Jan	1	0	0	5	0
EC F Jan	0	0	0	2	0
CO F Jan	0	0	0	6	0
EM F Jan	1	0	0	9	0
ET F Jan	0	0	0	0	0
AA F Jan	0	0	0	5	0
BO LF Jan	0	0	0	1	0
PC LF Jan	0	0	0	2	0
TF LF Jan	0	0	0	2	0
EC LF Jan	0	0	0	3	0
CO LF Jan	0	0	0	1	0
AA LF Jan	0	0	0	0	0
BO F Jan M	0	0	0	1	0
PC F Jan M	1	0	0	0	0
TF F Jan M	0	0	0	6	0
EC F Jan M	0	0	0	1	0
CO F Jan M	1	0	0	8	0
EM F Jan M	0	0	0	15	0
ET F Jan M	0	0	0	10	0
AA F Jan M	0	0	0	1	0
BO F May	1	0	0	1	0
PC F May	0	0	0	1	0
TF F May	0	3	0	2	0
EC F May	0	0	0	0	0
CO F May	0	1	0	1	0
EM F May	0	1	0	5	0
ET F May	0	1	0	1	1
AA F May	0	1	0	0	0
BO LF May	0	0	0	0	0
PC LF May	0	0	0	0	0
TF LF May	0	0	0	0	0
EC LF May	0	0	0	2	0
CO LF May	0	0	0	1	0
AA LF May	0	0	0	0	0

Appendix 5 continued

Sample	Eumolpinae	Tychiinae	Apionidae	Galerucinae	Elateroidea	unidentified Coleoptera
BO F Aug	4	0	0	0	0	0
PC F Aug	1	0	1	0	0	2
EC F Aug	0	0	0	0	0	0
CO F Aug	0	0	1	0	0	0
EM F Aug	0	0	2	0	0	0
ET F Aug	4	0	0	0	0	0
AA F Aug	0	0	0	0	0	0
BO LF Aug	0	0	0	0	0	0
PC LF Aug	0	8	2	0	0	0
EC LF Aug	0	0	1	0	0	0
CO LF Aug	0	0	0	0	0	0
AA LF Aug	0	0	1	0	0	0
BO F Jan	0	0	0	0	0	1
PC F Jan	1	0	0	0	0	0
TF F Jan	0	0	0	0	0	0
EC F Jan	0	0	0	0	0	1
CO F Jan	2	0	0	0	0	1
EM F Jan	0	0	0	0	1	1
ET F Jan	0	0	0	0	0	1
AA F Jan	2	0	0	0	0	0
BO LF Jan	3	0	0	0	1	0
PC LF Jan	2	0	0	0	0	1
TF LF Jan	1	0	0	1	0	0
EC LF Jan	3	0	0	0	2	0
CO LF Jan	1	0	0	0	3	1
AA LF Jan	0	0	0	2	0	0
BO F Jan M	0	0	0	0	1	0
PC F Jan M	2	1	0	0	0	0
TF F Jan M	0	0	0	0	0	0
EC F Jan M	1	0	14	0	0	0
CO F Jan M	7	0	0	0	0	1
EM F Jan M	3	0	0	0	0	0
ET F Jan M	2	0	0	0	0	0
AA F Jan M	0	0	0	0	0	1
BO F May	1	0	0	1	0	1
PC F May	0	0	0	0	0	1
TF F May	0	0	0	0	0	0
EC F May	0	0	0	0	0	0
CO F May	0	0	1	0	0	0
EM F May	0	0	1	0	0	2
ET F May	0	0	0	0	0	0
AA F May	0	0	0	0	0	0
BO LF May	1	0	0	0	0	0
PC LF May	0	0	0	0	0	0
TF LF May	1	0	0	0	0	1
EC LF May	0	0	9	0	0	0
CO LF May	0	0	0	0	0	0
AA LF May	0	0	0	0	0	0

Appendix 5 continued

Sample	Phasmatodea	Lepidoptera
BO F Aug	0	2
PC F Aug	0	7
EC F Aug	0	3
CO F Aug	0	2
EM F Aug	0	1
ET F Aug	0	2
AA F Aug	0	2
BO LF Aug	0	2
PC LF Aug	0	6
EC LF Aug	0	0
CO LF Aug	1	2
AA LF Aug	0	10
BO F Jan	0	0
PC F Jan	0	1
TF F Jan	0	1
EC F Jan	0	3
CO F Jan	0	5
EM F Jan	0	1
ET F Jan	0	0
AA F Jan	0	0
BO LF Jan	0	0
PC LF Jan	0	2
TF LF Jan	0	0
EC LF Jan	0	2
CO LF Jan	0	2
AA LF Jan	0	2
BO F Jan M	0	0
PC F Jan M	0	1
TF F Jan M	0	0
EC F Jan M	0	1
CO F Jan M	0	6
EM F Jan M	0	4
ET F Jan M	0	0
AA F Jan M	0	0
BO F May	0	0
PC F May	1	8
TF F May	0	3
EC F May	0	7
CO F May	0	0
EM F May	0	10
ET F May	0	2
AA F May	0	1
BO LF May	1	1
PC LF May	1	12
TF LF May	0	1
EC LF May	0	16
CO LF May	1	7
AA LF May	0	9